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Ecosystem Gas Exchange in Natural and Created Tidal Salt Marshes of Tidewater, Virginia

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**Ecosystem Gas Exchange in Natural and Created Tidal Salt Marshes of Tidewater,
Virginia**

**A Thesis
Presented to**

**The Faculty of the School of Marine Science
The College of William and Mary**

**In Partial Fulfillment
Of the Requirements for the Degree of
Masters of Science**

**By
Molly Mitchell Roggero
2003**

APPROVAL SHEET

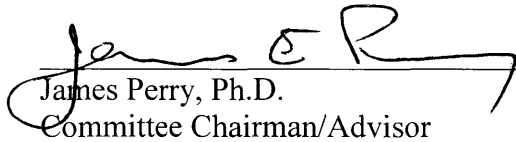
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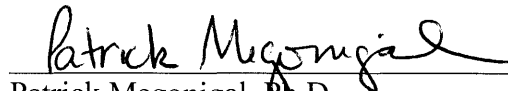
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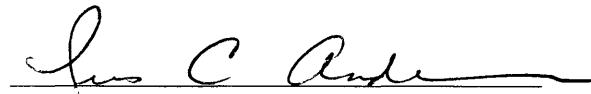
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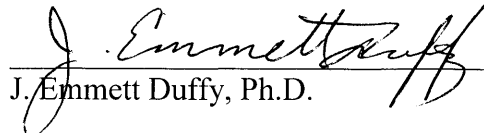

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Table of Contents

Abstract.....	Page 4
Chapter 1: A review of tidal salt marsh ecology.....	Page 5
Chapter 2: Ecosystem gas exchange in created and natural salt marshes.....	Page 32
<u>Figures</u>	
Figure 1: Map of study sites.....	Page 51
Figure 2: Sampling diagram	Page 52
Figure 3: Biomass.....	Page 53
Figure 4: SOM profiles.....	Page 54
Figure 5: SOM vs. Age.....	Page 55
Figure 6: Porewater nutrients.....	Page 56
Figure 7: Annual CO ₂ fluxes.....	Page 57
Figure 8: Monthly NEE.....	Page 58
Figure 9: Created vs. Natural NEE.....	Page 59
Figure 10: GPP:R ratio.....	Page 60
<u>Tables and Appendix</u>	
Table 1: ANOVA of Biomass and SOM.....	Page 61
Table 2: Correlation coefficients.....	Page 62
Table 3: ANOVA of Porewater nutrients.....	Page 63
Table 4: ANOVA of P, R, and NEE.....	Page 64
Appendix 1: Specific hypotheses.....	Page 65
Appendix 2: Chamber method.....	Page 68
Appendix 3: PAR and temperature for 2001.....	Page 71
Appendix 4: Sampling dates.....	Page 72

**Ecosystem Gas Exchange in Natural and Created Tidal Salt Marshes of
Tidewater, Virginia**

ABSTRACT

Tidal wetlands are an important feature of coastal systems that are frequently impacted or destroyed by coastal development. Wetland creation is one method of mitigating for the loss of natural wetlands; however, created wetlands may not replace the original, natural wetlands in some or all of their functions. In this study, we compared the function of created and natural tidal saltmarshes in terms of photosynthesis (P), respiration (R), porewater nutrients, and soil characteristics. P and R rates were used to model annual Gross primary production (GPP). Neither soil characteristics nor porewater nutrient levels were found to consistently differ between created and natural salt marshes. Total annual GPP did not vary between the two types of marshes; however, there was variation between late fall production in some created and natural marshes. This variation may reflect differences in ecological processes between the created and natural marsh types.

Chapter 1

A review of tidal salt marsh ecology

Introduction

Tidal wetlands are an important feature of coastal systems. They can absorb floodwaters or filter toxins and excess nutrients from streams (Mitsch and Gosselink 1993). However, they are frequently impacted or destroyed by coastal development. Wetland creation is one method of mitigating for the loss of natural wetlands and involves the conversion of upland area to marsh, or planting a marsh on dredge spoils. These created marshes may have similar plant communities, soils and hydrologic cycles to natural wetlands, but they are always young in terms of successional development compared to natural marshes. Therefore, created wetlands may not replace the original, natural wetlands in some or all of their functions.

Previous research on the development of natural ecosystem function within created marshes has focused primarily on structural characteristics and pool sizes. Certain characteristics appear to become similar to natural systems fairly quickly, such as above and belowground biomass of *Spartina alterniflora* (Broome et al. 1986, Craft et al. 1999) and nekton use (Minello 2000). Porewater chemistry should also develop relatively quickly, because it is largely dictated by the hydrology of the marsh (Tyler and Zieman 1999). However, soil organic matter pools require decades to resemble natural marshes (Craft et al. 1988, 1989, 1991, *in press*, Langis et al 1991). Epifauna and infauna community development require soil organic matter, therefore, they can take a relatively long period of time to develop (Sacco et al. 1994, Levin et al. 1996, Scatolini and Zedler 1996). This order of ecosystem development is not much different from natural wetland ecosystem development, which suggests that created wetlands may change over time to function in a similar manner to natural wetlands.

In contrast to the large amount of work on changes in the structure of created wetlands, few studies have considered changes in basic ecosystems processes such as gas exchange. Odum (1969) hypothesized that an ecosystem in early succession should have a high (< 1) ratio of photosynthesis to respiration, while a more mature system should have a lower ratio ($\cong 1$). If this hypothesis holds for tidal marsh systems, we would expect to see a decrease in the P:R ratio of marshes with increasing age, and this pattern should also be apparent in created marshes of different ages.

The purpose of this study was to determine the rate at which the carbon cycle in created tidal wetlands matures. Specifically, we determined how certain processes such as primary production and respiration changed in concert with structural characteristics such as soil organic matter over time. Second, we determined whether created marshes become similar in function to natural tidal salt marshes as they mature.

Ecosystem Development in Salt Marshes

Ammonium cycling

Nitrogen is an important nutrient in marshes and vital for plant growth. It is a critical component of proteins and enzymes in the plants, and therefore, has the potential to impact plant function. Nitrogen levels have been found to affect plant productivity, biomass, morphology, and reproductive potential (Valiela 1983). In many marshes, nitrogen is the limiting factor to plant production. Fertilized plants can grow up to 3 times as much biomass as unfertilized plants (Sullivan and Daiber 1974). Plants can take up nitrogen in two forms, NH_4^+ (ammonium) and NO_3^- (nitrate). However, in wetland sediments, low oxygen limits the availability of NO_3^- , making NH_4^+ the primary plant nutrient.

NH_4^+ is produced in wetlands through two different processes: mineralization from organic N (or ammonification) and DNRA (dissimilatory nitrate reduction to ammonia). Ammonification is a microbially-mediated process in which PON is mineralized to NH_4^+ . Since mineralization requires the presence of organic matter, it is spatially and seasonally affected by the distribution of labile organic matter. NH_4^+ concentration tends to be highest in the top 5 cm of the soil (where labile PON is highest) and decrease exponentially with depth (Tobias et al. 2001). Peak mineralization rates tend to occur in the fall, when senescing plants increase the supply of PON (Anderson et al. 1997, Neubauer et al. 2000). DNRA is also a microbially mediated process in which nitrate is reduced to NH_4^+ . The rate of DNRA can be affected by changes in the microbial community (often seasonal), the amount of NO_3^- entering the system, and the lability of the DOC substrate required for the conversion (Tobias et al. 2001). This process may be unimportant in a marsh with low NO_3^- input (Anderson et al. 1997).

There are several potential sources of nitrogen for a salt marsh, including nitrogen fixation, tidal flows, rainfall, streamflow, and groundwater (Valiela 1983). NO_3^- typically enters a system through groundwater or streamflow, and is reduced to NH_4^+ through DNRA. Increased DNRA rates result in increased nitrogen retention in the marsh system in the form of NH_4^+ (Tobias et al. 2001). In marshes where there is low input of NO_3^- , recycling of NH_4^+ appears to be an important process (Langis et al. 1991; Anderson et al. 1997). In these systems, high gross mineralization rates result in rapid turnover of sediment NH_4^+ (Anderson et al. 1997). Studies have shown the long term retention of NH_4^+ pools in the sediment, suggesting that this could be an important source of nitrogen in the marsh (White and Howes 1994; DeLaune et al. 1983). Plants only require nitrogen during the growing cycle, but NH_4^+ is produced throughout the year (Anderson et al. 1997). The extra NH_4^+ may be temporarily immobilized in bacterial biomass

during the winter months; than the highly labile PON is mineralized when the plants need NH_4^+ during the growing season.

Nitrogen loss from salt marshes is primarily as a result of the denitrification pathway, resulting in N_2 gas that diffuses into the air. However, studies have suggested that under certain conditions, marshes can export NH_4^+ into tidal waters (Page et al 1995; Chambers et al. 1992). The release of NH_4^+ into tidal waters may be related to the degree of vegetation on the site (Page et al. 1995). Unvegetated creek banks can also release NH_4^+ into overlying water during certain seasons (Anderson et al. 1997). The nitrogen being released from the marshes as NH_4^+ is probably not a significant loss to the marshes or a significant source to the estuaries (Howes and Goehringer 1994; Whiting and Childers 1989).

Nutrient cycling is of interest in created marshes because the presence and efficiency of nutrient cycling affects both the development and maintenance of marshes (Langis et al. 1991). Nitrogen is of particular interest because it is frequently the primary limiting nutrient in marshes. Studies of created marshes suggest that after 4-5 years, NH_4^+ pools are still significantly lower than those in natural marshes (Craft et al. 1991; Langis et al. 1991). Specific mineralization rates are similar between the two types of marshes, suggesting that the differences in nutrient pools are primarily due to differences in labile organic matter pools (Langis et al. 1991). There is no consensus as to how long it will take nutrient pools in created marshes to become similar to those in natural marshes, and it will probably depend on the rate of soil formation in the created marshes.

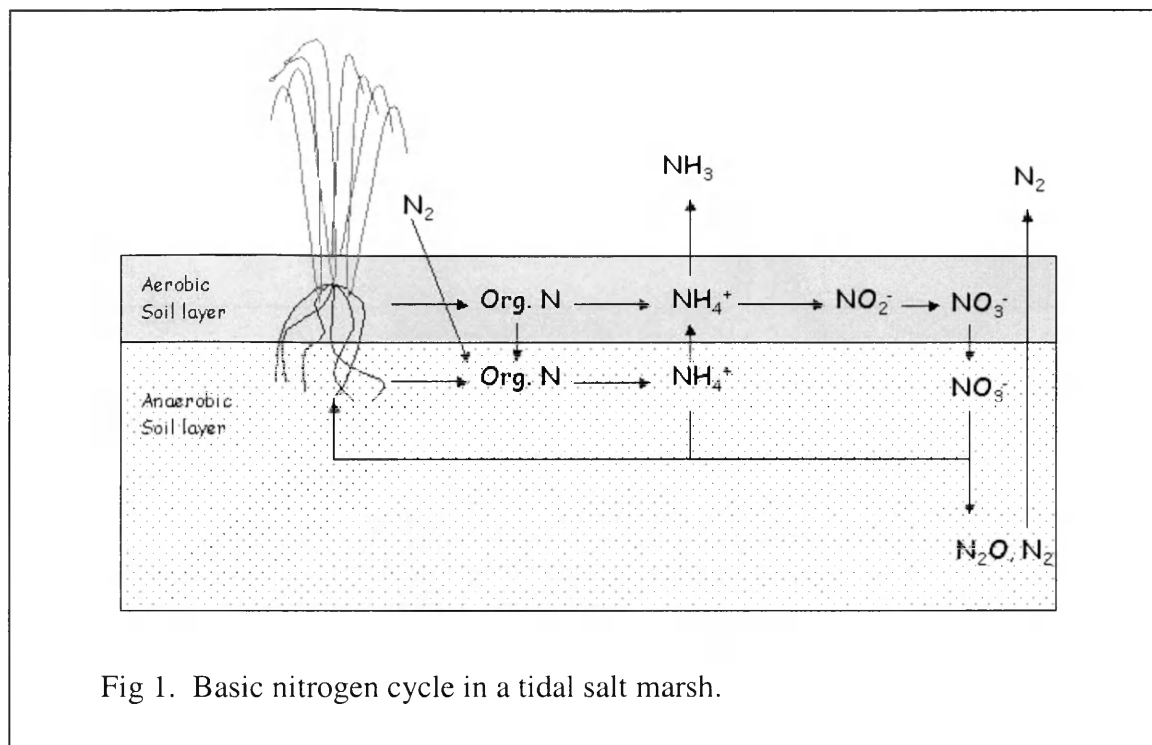


Fig 1. Basic nitrogen cycle in a tidal salt marsh.

Pedogenesis

Soil characteristics of salt marshes may change over time. Unlike terrestrial systems, wetlands tend to accumulate large amounts of organic matter (Craft 2000). Because of this, wetland soils may grow upwards (Craft 2000), not downwards like terrestrial systems. Geologically young marshes tend to have high soil bulk density, low organic carbon, and no organic-rich soil horizon (Craft et al. 1999). The high production in salt marshes contributes to the formation of organic rich soil, which lowers the bulk density over time. The time required for an organic rich surface layer to form depends on the duration and frequency of inundation, the net primary production of the emergent vegetation, the tidal amplitude, and the rate of sea level rise (Craft 2000). The organic matter content of a marsh affects the redox potential,

infaunal composition (Moy and Levin 1991), microbial remineralization rates, nitrification, denitrification, and N₂ fixation (Piehler et al. 1998). Percent silt, clay, and nitrogen content of the soil also tends to increase as the marsh ages, while the percent sand tends to decrease (Tyler and Zieman 1999). The soil composition, and the rate of change of the soil composition, can be affected by the deposition rate of sediment onto the surface of the marsh and the rate of decomposition of plant material. The rate of deposition of sediment is influenced by elevation (Pethick 1991) and plant density (Stumpf 1983), both of which can vary across a single marsh. High plant density slows water velocity, resulting in higher deposition of soil. As sediment deposition increases, hydraulic conductivity decreases; this decreases nutrient flushing and redox potential in the sediment by limiting aeration (Tyler and Zieman 1999). In naturally developing marshes, sediment grain size generally decreases over time (Osgood and Zieman 1993).

Succession in Salt Marshes

Salt marsh development and succession are affected by the hydrology (which depends on the landscape) and local physical forces acting on the marsh. The hydrology of the salt marsh dictates the chemistry of the porewater, and determines which flora and fauna can survive in the marsh (Tyler and Zieman 1999). Physical forces can also affect the chemistry of the porewater by determining the flushing time. Increased flushing of the pores has been linked to many factors that control *Spartina alterniflora* growth, such as increased sediment aeration (Agosta 1985), increased nutrient supply (Osgood and Zieman 1998), decreased salinity (Broome et al. 1986), and decreased sulfide concentrations (King et al. 1982). Some characteristics, such as salinity, also vary throughout the year. Porewater salinity tends to be higher in the late summer when high temperatures result in high evapotranspiration (Tyler and Zieman 1999). On the

Atlantic Coast, changes in species composition of the flora cannot be used to characterize salt marsh succession since *S. alterniflora* is both the pioneer and climax species in the low marshes (Tyler and Zieman 1999). Succession occurs primarily in the sediments. The macrophyte species composition will only change if there is a change in relative sea level. However, there are possible morphological changes in the plant community with age. One study (Tyler and Zieman 1999) showed an older marsh to have taller plants with more flowering structures. They also found that the percent nitrogen in the plant tissue increased significantly with age and was related to an increase in porewater ammonium concentrations (Tyler and Zieman 1999).

Comparing Natural and Created Marshes

Timeline of Created Marsh Development

In created salt marshes, different characteristics may reach the functional level of natural marshes in different amounts of time. Functions seem to develop in the following order: first the characteristics related to hydrology, then characteristics related to primary production, and last, soil characteristics (Craft et al. *in press*) The first characteristic to reach natural levels is the use of the marsh as nekton habitat. Created marshes appear to reach their maximum habitat support of nekton in less than 1 year (Minello 2000). The next characteristic of marshes to reach natural levels is the above-ground biomass of *S. alterniflora* (Broome et al. 1986, Craft et al. 1999). Above-ground biomass generally becomes equivalent to the biomass in natural systems within 2-4 years after creation. This is closely followed by the development of the belowground biomass within 3-5 years after creation (Broome et al. 1986, Craft et al. 1999). Once the macrophyte community has become established, the constructed marshes may have greater above-ground

biomass than the natural ones (Craft et al. 1999). The epifauna and infauna communities develop more slowly than the plant community. It can take as little as 5 years (Craft et al. *in press*) and as many as 17 years for these communities to develop in created marshes (Sacco et al. 1994, Levin et al. 1996, Scatolini and Zedler 1996). Infaunal community was significantly related to the percent organic matter of the sediment and silt/clay content of the soil in the marsh (Craft et al. *in press*). Biogeochemical processes such as organic matter and nutrient accumulation may take even longer to develop (Craft et al 1988, 1989, 1991, *in press*, Langis et al. 1991). Sediment organic matter may take 10-20 years to match natural levels (Piehler et al. 1998). The C:N ratio of the soil takes 10-25 years to reach levels equivalent to those in the natural marshes (Craft et al. 1999).

In created marshes, biomass accumulation appears to be greatest during the early and middle stages of ecosystem development, and it peaks within the first decade (Craft et al. 1999). Organic carbon and nitrogen content of the soil increases over time (Craft et al. 1999). Macro organic matter also increases with marsh age (Craft 2000). Since organic matter has low particle density (Craft et al. 1993), the soil bulk density decreased over time as the organic matter increased. The C:N ratio of the soil increased with age (Craft et al. 1999) as did the porewater ammonium. The density of the infauna (Craft et al. 1999), benthic invertebrates, and sub-surface deposit feeding oligotrophs (Craft 2000) increased over time, and with increasing soil organic carbon levels.

Differences Between Created and Natural Marshes

In theory, after a sufficient time period, a correctly designed constructed salt marsh will eventually become similar to natural marshes; however, recent studies indicate that some

functions may never reach natural levels, while others may exceed natural levels. Nutrient levels may be very different between created and natural marshes, even after long time periods. After 15 years, one created salt marsh still had less nitrogen, phosphorus, and organic carbon than natural marshes (Craft et al. 1988). Nitrogen accumulation was 2-5 times higher in the created marshes (Craft et al. 1999). One created marsh had very low denitrification rates, possibly because it had coarser sediments than the natural marsh, and therefore less surface area for microbial populations, greater porewater flushing, and more exposure to oxygen (Thompson et al. 1995). Created marshes can also have greater redox potentials (Craft et al. 1991, Thompson et al. 1995). Again this may be due to the coarseness of the grain compared to natural sites. Polychaete and crustacean densities may differ between created and natural marshes (Streever 2000). The development of the benthic invertebrate community depends on the formation of wetland soil characteristics (Craft 2000). Infauna density was found to be 70-330% higher in created marshes than in natural marshes (Craft et al. 1999). The created marshes also had significantly higher densities of surface deposit feeders (Craft et al. 1999). As fish habitat, created marshes have mixed results. For commercially important fishery species, even the older created marshes function at a lower level than natural marshes (Minello 2000). However, gut content analysis indicated that some of the fish feeding in a created salt marsh were eating food that was nutritionally superior to those found in adjacent natural salt marshes (Moy and Levin 1991). Created and natural marshes may also have different physical characteristics. One study found natural salt marshes to have undulant marsh-water edges, island like *S. alterniflora* plant stands, concave shorelines, and low elevations (Delaney et al. 2000). The created marshes tended to have smooth marsh-water edges, unbroken shorelines, convex or straight shorelines, and higher elevations (Delaney et al. 2000).

There are many factors that do appear to approach natural levels over time. Species richness and the trophic composition of the infaunal communities are the same in older created and natural sites (Craft et al. 1999). Within five years of creation, net primary production has been found to be similar to natural sites (Broome et al. 1986). However, in some marshes it may take more than twice that amount of time for *Spartina* biomass and stem height to equilibrate to natural levels (Craft et al. *in press*). After 25 years, created marshes had similar macrophyte production and organic carbon and nutrient accumulation (Craft et al. 1999). In addition, the percent of net primary production that was buried was also similar (Craft et al. 1999). N₂ fixation and chlorophyll a concentration were unusually high in the surface sediment of a 1 year old marsh, but had decreased to natural levels by 6 years of age (Piehler et al. 1998). This may be due to increasing stem density with age, which reduced light levels on the marsh surface. Also, low nitrogen levels and the sandy soils in the young marsh may create a better surface for growing cyanobacteria (Piehler et al. 1998). In other marshes studies, the chlorophyll a concentration took up to 15 years to develop (Craft et al. *in press*).

Carbon Cycling in Wetlands

Carbon enters the wetland cycle through the process of photosynthesis (in the form of CO₂), both by plants and algal mats. The carbon is stored in both above-ground and below-ground biomass. A certain amount of the carbon fixed during photosynthesis is returned to the atmosphere as CO₂, the end product of plant respiration. At the end of the growing season, above-ground biomass senesces and falls to the marsh surface, where it can be exported as DOC or buried. There are two possible pathways for carbon in marsh sediments: labile carbon will be mineralized to CO₂, DIC, or CH₄ or refractory carbon will be buried and add to marsh accretion.

CO₂ is produced through both autotrophic and heterotrophic respiration under both aerobic and anaerobic conditions. Both CO₂ and CH₄ can be returned to the atmosphere through diffusion, ebullition or movement through continuous gas spaces in plant stems (Smith et al. 1983). Some CO₂ can also be recycled and taken up by marsh plants during photosynthesis (Smith et al. 1983).

Photosynthesis results in the fixation of carbon from the atmosphere into the plant community. It is the major source of carbon into the marsh system. In some cases, terrestrial carbon is imported into marshes (McKenna 2003), but this is unlikely to be an important source of carbon in most systems. Net photosynthesis varies throughout the year, in the shape of a parabola, related to ambient light levels. The beginning of the growing season is generally in March or April, and net photosynthesis increases until it reaches a maximum value in the mid-summer when it begins to decline (Miller et al. 2001; Mann and Wetzel 1999; Drake and Read 1981). The decline in net photosynthesis in the late summer and early autumn has been attributed to individual plant metabolism, such as photorespiration (Mann and Wetzel 1999), and community dynamics, such as canopy structure (Turitzin and Drake 1981). It may also be due to small spring leaf area and senescing leaves in the autumn (Wickland et al, 2001). Rates of photosynthesis are affected by changes in salinity, elevation, and soil Eh. Rates of CO₂ fixation decline under conditions of high salinity and low Eh (Pezeshki and DeLaune 1995; Pezeshki and DeLaune 1993). Increased elevation tends to lead to increased soil aeration, which raises soil Eh and increases photosynthetic rates (Bouchard and Lefevre 2000; Pezeshki et al. 1992).

Community respiration is the major loss of carbon from the marsh system. It is composed of two components: plant respiration and microbial respiration. Carbon can also be lost through tidal export, but this does not seem to be important in most systems (Bouchard and

Lefeuvre 2000). Community respiration is related to temperature (Wickland et al. 2001), and is highest in the mid-summer (when temperatures are highest), and is lower in the spring and autumn (Drake and Read 1981; Wickland et al. 2001). Respiration occurs throughout the day and night, in contrast to photosynthesis which only occurs during daylight hours. Nighttime respiration can account for the loss of 34% of daily carbon uptake (Drake and Read 1981). Community respiration is affected by water level and salinity. Lower water tables allow for greater sediment oxidation leading to increased microbial metabolism and also may decrease plant stress (Nyman and DeLaune 1991). Community respiration is highest in freshwater marshes and lowest in brackish water communities; probably due to high soil porosity in freshwater marshes combined with decreased lability of organic matter in brackish marshes (Nyman and DeLaune 1991).

Plant respiration can account for 50% of community respiration in the dark (Howes et al. 1985). However, the percent may vary from marsh to marsh due to differences in above and below ground production and the relative percent of carbon buried or exported from the marsh. CO₂ from respiration in aboveground plant parts is released directly in to the atmosphere; root and rhizome can release CO₂ into the sediment, but generally use plant lacunae to vent it to the atmosphere (Howes et al. 1985). Plant respiration is correlated with the nitrogen content of the plant (Ryan 1991; Reich et al. 1998). Rhizome respiration rates are affected by nutrient supply and age. Respiration rates tend to increase as nutrient supply increase and by-products of increased respiration may be coupled to increased ammonium assimilation (Cizova and Bauer 1998). Rhizome respiration rates tend to decrease with age as metabolically active tissue is replaced by starch (Cizova and Bauer 1998). The exception to this rule is in the springtime,

when the stored energy in the rhizomes is translocated to growing shoots, leading to higher respiration in the oldest rhizomes.

Soil CO₂ production is primarily mediated by microbes and is a measure of the rate of organic matter decomposition in the soil. About 80% of belowground production is decomposed in situ to CO₂ (Howes et al. 1985). Soil processes account for 10-20% of ecosystem respiration (Miller et al. 2001). Soil CO₂ production is positively related to mean monthly temperature and tends to peak in the mid-summer and then decline (Miller et al. 2001, Howes et al. 1985). However, CO₂ production is higher in the fall than in the spring, probably due to increased organic matter input to the sediments in the fall (Howes et al. 1985). Soil respiration is affected by marsh inundation and plant rhizome quality. Increased inundation tends to decrease soil respiration (Miller et al. 2001). The high sugar content of certain types of *Spartina alterniflora* plants increases microbial respiration rates because sugar is more labile than starch (Seliskar et al. 2002).

Net ecosystem exchange (NEE) is the balance between carbon assimilated into the marsh system and the carbon lost from the system. NEE is an important variable in wetland stability (Nyman et al. 1990). In times when wetlands remove more carbon from the atmosphere than they release, this carbon can be stored in the wetland as peat, and help the wetland keep up with rising sea levels. Oxidation of the peat can result in the loss of this stored carbon through increased microbial respiration. Wetlands can be both sources and sinks for carbon, and may show large inter-annual variability (Wickland et al. 2001). Whether a particular wetland is a source or a sink for carbon can also vary spatially across the marsh (Miller et al. 2001).

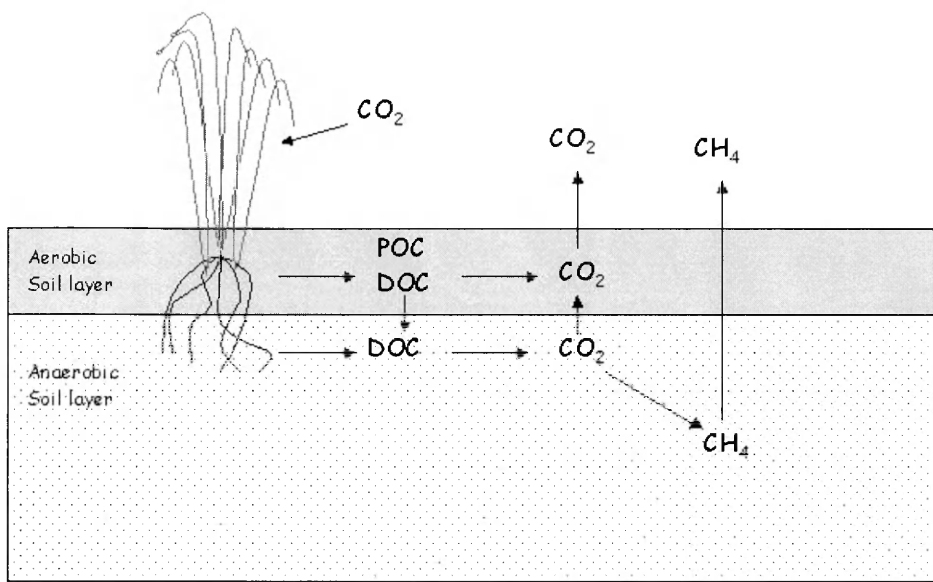


Fig 2. The basic carbon cycle in tidal salt marshes.

Spartina alterniflora Marshes

General Characteristics

S. alterniflora is a member of the grass family that grows in tidal salt water marshes along the eastern coast of the United States. In Atlantic coastal salt marshes, local gradients in *S. alterniflora* production are usually found (King et al., 1982). There is a tall form and a short form, as well as intermediate forms. *S. alterniflora* height and biomass are generally greatest on the banks of the feeding streams; this is where the tall forms are found. The short form is generally found in the interior of the marsh. The tall form has 3 to 5 times the annual production

of the short form, and can account for 30-50% of total marsh production (King et al. 1982).

There are two main factors that appear to affect plant growth: soil water movement and porewater sulfide concentrations (King et al. 1982), although other factors may also be important. The relationship between these two factors is not clear, but it has been suggested that at the plant level the major growth limiting factor is sulfide concentrations, while at the ecosystem level, the major limiting factor is soil water movement (King et al. 1982). Soil water movement tends to be highest in areas with tall forms. These areas show both vertical and lateral water movement and presumably result in high flushing of the pore spaces. Areas with short forms tend to show little to no water movement and presumably have poor flushing. Redox profiles are correlated with plant height in the marsh (King et al. 1982). Sulfide concentration in porewater is inversely correlated with soil water flow and plant production (King et al. 1982). Tall forms are also typically found in areas with lower salinity than the short forms (Bagwell et al. 1998). Zinc and copper concentrations were found to be higher in the tissues of the short form of *S. alterniflora* (Ornes et al. 1998). It is possible that excess copper may be toxic to this plant, causing reduced growth (Waddell and Kraus 1990). The difference in zinc concentration may simply be due to phosphorus limitation in the marshes with the short form. It has been suggested that high phosphorus concentration in the tissues may prevent the plant from taking up zinc; all the short forms had low phosphorus (and high zinc), while the tall forms showed the opposite pattern (Ornes et al. 1998). There does not appear to be any difference between the amount of Mn and iron in the tissues of the tall and short forms (Ornes et al. 1998).

Effects of HS⁻ on S. alterniflora growth

Excess sulfide is toxic to plants. High levels of sulfide in porewater reduce the efficiency of nitrogen uptake by the plants (Bagwell et al. 1998). Reduced nitrogen uptake may result in decreased production for the plant and would lead to shorter forms of *S. alterniflora*. Sulfide also lowers O₂ availability in the soil (King et al. 1982). This may cause the roots to shift from oxidative metabolism to fermentative metabolism. Fermentative metabolism results in less energy for the plant to use for nutrient uptake and growth (King et al. 1982), and could result in the shorter form. It is interesting that there does not appear to be any correlation between the rate of bacterial sulfate reduction and the growth form of the plant (King et al. 1982). It is possible that differences in the amount of hydrogen sulfide in the porewater are primarily due to differential precipitation of iron sulfides. Areas with tall growth forms will have more precipitation of iron sulfides because they have a larger pool of iron than the areas with the shorter forms of *S. alterniflora*. In addition, the formation of hydrogen sulfide requires anoxic conditions; taller plants may deliver more oxygen down to the rhizosphere.

Sulfur is an important redox element in aquatic systems and it is responsible for a number of important biogeochemical processes (Luther et al. 1986). Some of these processes are: sulfate reduction, pyrite formation, metal cycling, salt marsh energetics, and atmospheric sulfur emissions (Luther et al. 1986). In the salt marshes there are high sulfate concentrations (from seawater) and organic sulfur (from the plants). These and other forms of sulfur can be reduced to form sulfide in the anoxic zone of the soil (Fig. 3). In this process, low molecular weight organic carbon compounds tend to act as electron donors, and organic sulfur or sulfate act as the terminal electron acceptor. An example of this process is shown in the following equation (Mitsch and Gosselink 1993):



This reaction can occur over a range of pH, but it occurs at the fastest rate at neutral pH (Mitsch and Gosselink 1993). The resulting sulfide has two basic fates. If iron (II) is available, the sulfide may combine with the iron to form poorly soluble pyrite that is usually buried in the anoxic zone. The sulfide may also travel out of the anaerobic soil layer, up into the aerobic soil layer. Here the sulfide is re-oxidized to sulfate (or another form of sulfur). If the sulfide is not re-oxidized it may diffuse out of the soil and into the atmosphere. The balance between these processes can differ between marshes, soil depth and the time of the year. In one marsh (Luther et al. 1986) they found that in warmer, more productive seasons, sulfur is transformed from inorganic to organic species; and in colder, less productive times, sulfur is transformed from organic to inorganic forms.

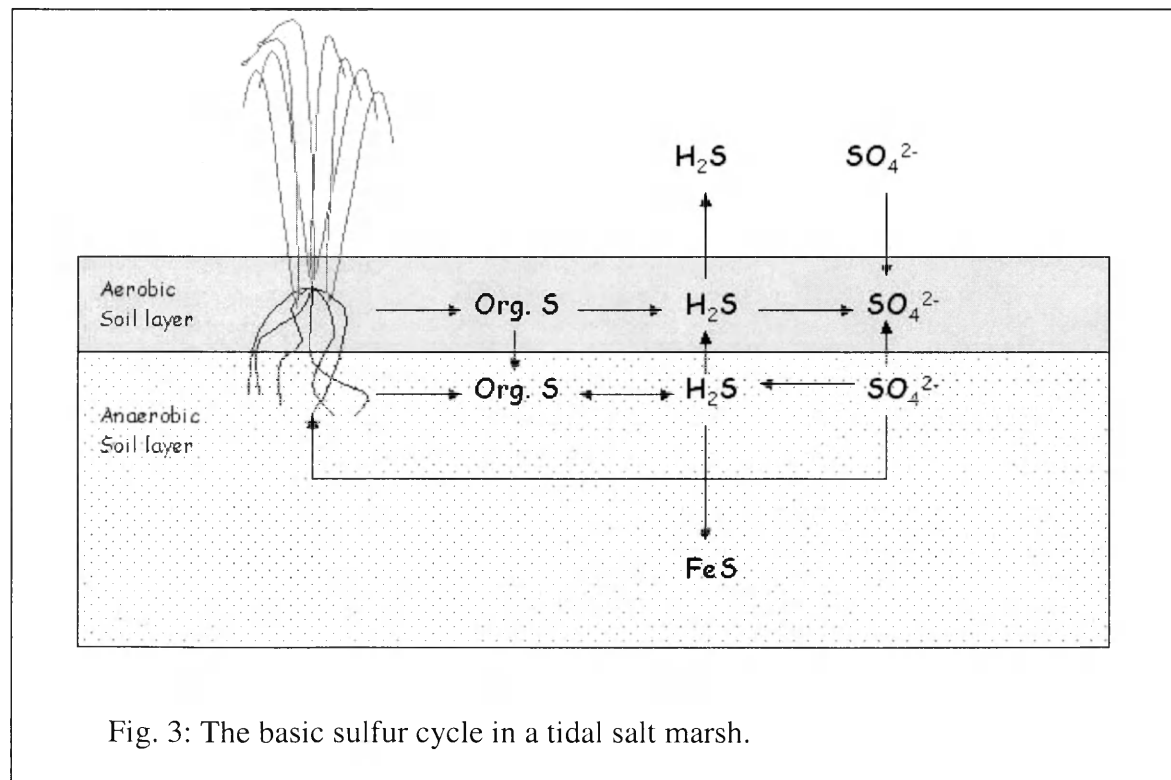


Fig. 3: The basic sulfur cycle in a tidal salt marsh.

Changes in the rate of sulfate reduction over the year is important since the end products of sulfate reduction are reactive and influence the chemical composition of the sediment (Hines

et al. 1989). Therefore, they have the potential to affect many factors of the ecosystem including plant growth. Plant growth, in turn, can influence sulfate reduction by releasing organic compounds into the soil. Plants can also influence sulfate reduction by changing redox potentials in the soil through the enhancement of gas diffusion and evapotranspiration (Hines et al. 1989). Near the rhizomes, sulfate reduction tends to be highest in the summer months and decreases to its lowest rate in the fall; sulfide concentrations followed a similar pattern (Hines et al. 1983; Rooney-varga et al. 1997). In the summer, roots produce high quantities of carbohydrates when the plant is growing (Hines et al. 1989). In the late summer and early fall, carbohydrate production is reduced as the plants flower (Hines et al. 1989), resulting in a concurrent decrease in sulfate reduction activity. In the short forms of *Spartina alterniflora*, however, there are no apparent trends in sulfate reduction over the seasons. The short forms of the plant do not produce large amounts of new rhizomes during their aboveground growth spurt (Hines et al. 1989). This pattern was also not apparent in the bulk soil away from the rhizomes (Ramos et al. 2000).

Photosynthetic capacity

S. alterniflora is a C₄ plant; an adaptation that it shares with many plants that thrive in drought conditions. C₄ photosynthesis is a useful adaptation for a salt marsh plant because salt marsh soils have low water potential due to their high salt content (Mitsch and Gosselink 1993). Photosynthesis requires that the stomata be open during the process, this leads to high evapotranspiration, which can be a problem when water is not readily available. C₄ plants can withdraw CO₂ from the atmosphere until its concentration drops below 20 ppm; 10-60 ppm lower than C₃ plants (Mitsch and Gosselink 1993), and therefore are more efficient in their use of

CO₂ than C₃ plants. C₄ plants use PEP (phosphoenolpyruvate) as the CO₂ acceptor, which allows for the possibility of recycling of CO₂ from respiration (Mitsch and Gosselink 1993). C₄ plants can use much more intense sunlight for photosynthesis; C₃ plants usually reach their P_{max} at 1/2-1/4 of full sunlight intensity, while C₄ plants reach it near full intensity (Mitsch and Gosselink 1993). C₄ plants are more efficient users of water, have a lower respiration rate in the light, and have a higher temperature optimum (Mitsch and Gosselink 1993).

There do not appear to be any differences in photosynthetic capacity between the tall and the short forms of *S. alterniflora* (Dai and Wiegert 1997), although, the short form behaves as an intermediate between a C₃ and a C₄ plant (Mitsch and Gosselink 1993). Total net productivity was found to be much higher in the tall form than in the short form, possibly because the tall form tended to have higher leaf nitrogen (Dai and Wiegert 1997). Each additional mmol of leaf nitrogen can increase P_{max} up to 0.20 umol CO₂/m² leaf area/s in the summer time (Dai and Wiegert 1997). This suggests that differences in production between different populations may be due to differences in leaf nitrogen. Photosynthesis increases with increasing leaf nitrogen concentration and temperature up to a certain point, where it levels off (Dai and Wiegert 1997). In one study, P_{max} was found to never exceed 1000 umol/m²/s, and the Q₁₀ value for net leaf photosynthesis was 1.8 (Dai and Wiegert 1997). For an unshaded leaf in a tall population, photosynthetic capacity is most likely limited by leaf nitrogen in the summer and temperatures in the winter (Dai and Wiegert 1997).

The Hypothesis of Ecosystem Development

A new community goes through several stages of development before reaching a climax community. Each stage affects both the abiotic and the biotic factors of the next stage. The sequence of stages affects the plant and animal communities as well as the abiotic environment of the resulting ecosystem. To study ecological succession from the early stages usually requires a catastrophic event of some type that wipes out all organisms from an area and allows re-colonization. However, some factors (such as soil type) from the previous community remain and may influence the re-colonization event. Created wetlands offer a unique opportunity to examine the principles of ecological succession. In the creation process, the soil is usually stripped down to a subsoil, and the hydrology of the area altered. This allows a completely different type of ecosystem to form in place of the previous one.

The main principles of ecosystem succession were developed by Odum (1969). He included a number of hypotheses about the evolution of different parameters of ecosystems (production, diversity, complexity, etc.) during succession. Odum's (1969) definition of ecological succession consisted of three main principles. First, there is an orderly procession of community development that is generally directional and is, therefore, predictable. Second, community development results from changes in the physical environment caused by the community itself. Third, at the end of development, the community reaches a stable climax community.

Odum (1969) suggested that his hypothesis of the evolution of production could be used to assess the functional level of an ecosystem. In a young system, functional levels should be low, whereas in a climax community they should be high. During the late stages of succession there is a fundamental shift in energy flow as increasing flow is relegated toward maintenance. A stabilized ecosystem (one which is no longer developing) has reached a state of maximum

protection, or, the maximum support of the complex biomass structure. One way of evaluating the functional stage of an ecosystem would be to look at the ratio of gross primary production (P) to community respiration (R). In the early stages of succession, P should be greater than R--making the P/R ratio greater than one. As succession continues, and energy is redirected towards maintenance, the P/R ratio will decrease. In the climax community, P will be approximately equal to R and therefore, the P/R ratio will equal one. During early stages of succession (when $P > R$) there will be high production in the ecosystem (Odum, 1969). High production results in high levels of detritus, an important component in organic soil formation. By creating new soil, Odum's second principle (changes in the community result from changes in the physical environment, caused by the previous community) would be fulfilled. Research in forest ecosystems supports the theory that net ecosystem production will change with ecosystem maturation (Lichter 1998).

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Chapter 2

Ecosystem gas exchange in created and natural salt marshes of Tidewater, Virginia

INTRODUCTION

Tidal wetlands are an important feature of coastal systems. They can absorb floodwaters or filter toxins and excess nutrients from streams (Mitsch and Gosselink 1993). However, they are frequently impacted or destroyed by coastal development. Wetland creation is one method of mitigating for the loss of natural wetlands and involves the conversion of upland area to marsh, or planting a marsh on dredge spoils. These created marshes may have similar plant communities, soils and hydrologic cycles to natural wetlands, but they are always young in terms of successional development compared to natural marshes. Therefore, created wetlands may not replace the original, natural wetlands in some or all of their functions.

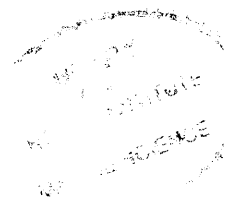
Previous research on the development of natural ecosystem function within created marshes has focused primarily on structural characteristics and pool sizes. Certain characteristics appear to become similar to natural systems fairly quickly, such as above and belowground biomass of *Spartina alterniflora* (Broome et al. 1986, Craft et al. 1999) and nekton use (Minello 2000). Porewater chemistry should also develop relatively quickly, because it is largely dictated by the hydrology of the marsh (Tyler and Zieman 1999). However, soil organic matter pools require decades to resemble natural marshes (Craft et al. 1988, 1989, 1991, Langis et al 1991). Epifauna and infauna community development require soil organic matter, therefore, they can take a relatively long period of time to develop (Sacco et al. 1994, Levin et al.

1996, Scatolini and Zedler 1996). This order of ecosystem development is not much different from natural wetland ecosystem development, which suggests that created wetlands may change over time to function in a similar manner to natural wetlands.

In contrast to the large amount of work on changes in the structure of created wetlands, few studies have considered changes in basic ecosystems processes such as gas exchange. Odum (1969) hypothesized that an ecosystem in early succession should have a high (< 1) ratio of photosynthesis to respiration, while a more mature system should have a lower ratio ($\cong 1$). If this hypothesis holds for tidal marsh systems, we would expect to see a decrease in the P:R ratio of marshes with increasing age, and this pattern should also be apparent in created marshes of different ages.

The purpose of this study was to determine the rate at which the carbon cycle in created tidal wetlands matures. Specifically, we determined how certain processes such as primary production and respiration changed in concert with structural characteristics such as soil organic matter over time. Second, we determined whether created marshes become similar in function to natural tidal salt marshes as they mature.

METHODS



Site Descriptions

The three sites used in this study each contained a created salt marsh immediately adjacent to a natural salt marsh (Fig. 1). The three created marshes represented a

chronosequence. At the time of sampling, the youngest was 4 years old (Air Power Park), the middle was 9 years old (Operation Smile) and the oldest was 22 years old (Goose Creek). All of the natural marshes are over 50 years old (Craft, unpublished data), and were considered to be mature.

Goose Creek (GC) is approximately 4 ha in size, was planted in 1980, and is surrounded on three sides by forest. It was originally planted with *S. alterniflora*, but has become primarily a *Phragmites australis* marsh. The natural marsh is less than 2 ha in size and is dominated by *Spartina alterniflora*. Tidal water enters the natural marsh system from the creek, and the created marsh through a channel that connects the marsh to Goose Creek. We established transects in both the created and natural marsh running perpendicular to the main tidal stream. The natural marsh transect community was primarily *S. alterniflora*; while the created marsh transect community was primarily *Scirpus robustus* with some *S. alterniflora*.

Operation Smile (OS) salt marsh was planted in 1992. It has a small forest buffer on the south side, a power plant on the north, and is approximately 1/2 ha in size. It was dominated by *S. alterniflora*, but was invaded by *Phragmites australis* around 2001. The natural marsh is primarily surrounded by residences. It is approximately 1 ha in size and the plant community is dominated by *S. alterniflora*. Tidal water enters the marsh system through a stream that dissects the natural marsh, then flows into the created marsh. Both transects in the created and natural marsh ran parallel to the tidal stream and consisted primarily of *S. alterniflora*.

Air Power Park (AP) salt marsh is about 1/2 ha in size and was planted in 1997. The natural marsh is approximately 2 ha in size. Both marshes are surrounded by a border of grass and shrubs. The water enters the marsh system through a stream in the natural marsh and then flows into the created marsh. Both created and natural marshes were both dominated by *S.*

alterniflora. Transects in both marshes ran perpendicular to the tidal stream and consisted primarily of *S. alterniflora*.

Experimental Design

One-20 m long transect was established in each marsh. To the extent possible, the transects within a pair of created and natural marshes were oriented the same way with respect to the tidal creek and elevation. All of the transects were located near the largest tidal creek for feeding the marsh. A 0.25 m² x 0.3 m deep aluminum base was permanently inserted into the ground at five randomly chosen plots along each transect. Bases were pushed into the ground until about 3 cm was left exposed, preventing water from accumulating inside the bases for any length of time. These bases sealed the ground off from airflow when a chamber was placed on top.

Net Ecosystem Exchange and Respiration Measurements

Carbon flux sampling began in October 2000 and ended in December 2001. Flux measurements were made at low tide and during the hours of highest light (usually 9 am to 4pm). We sampled once a month at each marsh using a transparent, enclosed chamber attached to a Li-COR 6400, a portable computer that is attached to an InfraRed Gas Analyzer (IRGA) (Fig. 2). The chamber was 0.25 m² at the base, and tall enough so that the plants would not be bent during flux measurements. The chamber was made of a lightweight aluminum frame covered with a transparent, heat-permeable plastic. It was open at the bottom where it attached to the base located at each plot. A door on the chamber could be opened to ventilate the inside of the chamber between measurements. During measurements, fans inside the chamber mixed the air.

The chamber was securely attached to the base with clamps. The Li-COR 6400 pumped air from the chamber into the IRGA, which measured the amount of CO₂ in the air and the air temperature; the air was then returned to the chamber. CO₂ measurements were taken at approximately 7 second intervals and the change in CO₂ was integrated over an appropriate (user-defined) time period to calculate the CO₂ flux. A positive change in CO₂ indicated net photosynthesis, and a negative change indicated net respiration.

At each plot, we made one set of 3-8 flux measurements at four light levels (100%, 50%, 25% and 0% of ambient). The length of each measurement varied between 15 s and 1 min, depending on the net rate of CO₂ flux at that time of the year. Low rates of net CO₂ flux required longer measuring times for accuracy. Light was manipulated by covering the chamber with screening. The 100% reading represented net photosynthesis at ambient light, while the 0% reading represented respiration of the plot. During the winter, when the plants were dead and no measurable photosynthesis was occurring, we only measured respiration.

The Li-COR 6400 logged photosynthetically active radiation (PAR) and soil temperature at the same user-defined intervals as net CO₂ flux. PAR was measured with a light meter located at the inside top of the chamber. An external soil probe was used to measure soil temperature.

Porewater nutrients

Porewater nutrients were sampled in the fall (October 2001), winter (January 2002) and spring (April 2002). We collected the porewater from 10-15 cm depth (about half-way into the root zone) using Push Point samplers. Samples were collected at plots 1, 3, and 5. Porewater [HS⁻] was preserved using zinc acetate and measured using titration (*Standard methods for the*

Examination of Water and Wastewater, 1971). Porewater $[\text{NH}_4^+]$ was measured using the phenolhypochlorite method (Solorzano 1969).

Plot Distance to the Creek

The distance of each individual plot to the nearest creek or channel was measured in each marsh. This was used as a co-variate in most analysis to ensure that differences between marshes were not entirely due to differences in transect placement.

Soil Characteristics

Soil cores were collected using a 2-inch diameter corer at each plot and at five random spots throughout each marsh. Compression was estimated using the core length relative to the hole depth. Each core was divided into 4 sections: 0-2 cm, 2-5 cm, 5-10 cm, and 10-20 cm, and each section was sub-sampled using a 30-mL syringe tube. The sub-sample size was 5 ml for the 0-2 and 2-5 cm sections, and 10 ml for the 5-10 and 10-20 cm sections. Larger samples were taken from the larger sections to ensure adequate representation of organic matter. Sediment organic matter was determined using loss-on-ignition. Sub-samples were oven dried at 50°C for 3 days, weighed, then ashed at 500°C for 5 hours, and re-weighed. The difference between the dry weight and the ashed weight represented the organic matter mass in the sample, which was expressed as a percentage of the total sediment dry weight.

Modeling Photosynthesis

We regressed CO_2 flux (dependent variable) against photosynthetically active radiation (PAR) for each set of measurements per plot. We used one of the following two models to fit the

regression. A linear equation ($y = y_0 + ax$) was used when net ecosystem exchange did not reach a P_{max} due to low PAR. At other times a hyperbolic equation ($y = y_0 + [ax/(b+x)]$) was used, where y_0 represented the CO_2 flux at $PAR = 0$ and a and b are parameters that describe the initial slope of the line and the value at which CO_2 flux ceases to change with a change in PAR (P_{max}), respectively.

We used LTER (Porter et al. Dataset ID: VCR97018) hourly measurements of PAR as the x value in the equations for each plot. PAR (Photosynthetically active radiation) and temperature readings used were taken on the Eastern Shore of Virginia during 2001. They should be very similar to the PAR levels and temperatures in Norfolk and Chesapeake, Virginia, but may differ somewhat from those in Hampton, Virginia, which is further from the coast than the other two sites. In addition, the PAR levels and temperatures were measured in an open, unshaded area, while the sites used in this experiment had forested areas around them.

Equations from the regressions were used to calculate instantaneous photosynthesis totals for each plot hourly based on the PAR data, then the instantaneous photosynthesis totals were summed for the entire month in each plot, giving GPP for the month. The monthly sums from each plot were summed over a 12-month period (Jan-Dec 2001) to get an annual total for each plot, which were then averaged for all five plots to get mean annual photosynthesis in each marsh.

Modeling Respiration

For each plot, in each marsh, we regressed respiration values (net CO_2 flux when $PAR = 0$) against hourly air temperature using annual data. We used air temperature rather than soil temperature, because hourly soil temperatures were not available from the LTER database. The

Ahrennius equation was used for the regression model, where $\ln(\text{CO}_2 \text{ flux})$ was the dependent variable and $1/\text{temperature (in K)}$ was the independent variable. In general, we used an equation based on the respiration over a year in a single plot. When these regressions were not significant, we used an equation representing the respiration for the entire marsh over a year. In one case, we used soil temperature versus respiration in the model because neither the per-plot equation nor the per-marsh equation was significant when air temperature was used.

The regression equations were used to calculate a Q_{10} value for each plot as follows: $Q_{10} = \text{CO}_2 \text{ flux rate @ } 20^\circ\text{C} / \text{CO}_2 \text{ flux rate @ } 10^\circ\text{C}$. Q_{10} s ranged from 4.6 to 1.7, with an average of 2.8. Q_{10} values were then used to calculate the hourly respiration values for each plot: for each month, we calculated a mean respiration value and a mean temperature value for each plot, based on the actual field measurements. These mean values were inserted in to the Q_{10} equation to calculate hourly respiration. We used LTER (Porter et al. Dataset ID: VCR97018) hourly measurements of temperature and calculated the change in temperature from the mean of our field measurements for every hour. Q_{10} values were used to relate the change in temperature from the field measurements to a change in respiration rate. The hourly respiration values were summed for the entire month in each plot.

Calculating Net Ecosystem Exchange

NEE was calculated for each plot using the following equation: $\text{NEE} = \text{GPP} - \text{R}$, where GPP is monthly net photosynthesis and R is monthly total respiration. We averaged all plots in each marsh to get a mean monthly modeled NEE value (NEE_m). Annual NEE for each marsh was calculated as the sum of NEE_m between Jan-Dec 2001.

Statistical Analysis

Distance from the plots to the creek was measured as a proxy for the length of inundation at a plot and the amount of flushing that occurs in the porewater of the sediment. Since both length of inundation and the amount of flushing can affect plant growth and porewater nutrients, and because some variables were correlated with distance from the creek, we used this measure as a co-variate in the analysis.

Biomass, P, R, NEE, and salinity were analyzed using two-way ANOVAs with marsh site and type as fixed factors and distance to creek as a covariate. $[\text{NH}_4^+]$ and $[\text{HS}^-]$ were analyzed using a MANOVA (all 3 samplings analyzed concurrently) with marsh site and type as fixed factors and distance to creek as a covariate. Correlations were run between variables that we believed should be related. GPP:R ratio was analyzed both un-normalized and normalized by plot distance from the creek because the two variables were highly correlated.

Only biomass samples from October 2001 were included in the statistical analysis because they were taken from the same plots and during the same growing season as the CO_2 flux measurements. Natural log transformations were conducted when necessary, to ensure that data met the requirements for normality and homoscedasticity. Significant differences were established at $p < 0.05$.

RESULTS

Above-ground Biomass

Biomass increased throughout the growing season at all sites (Fig. 3). In October 2001, biomass was significantly correlated with the distance of the plot from the creek, but did not

differ significantly by either marsh site or type (Table 1). At both Air Power Park (AP) and Operation Smile (OS), the created marsh had higher October biomass than the natural marsh, while biomass in the natural and created marshes at Goose Creek were similar. The difference in biomass between the created and natural marshes at AP was not statistically significant when distance to water was factored into the analysis as a covariate. All plots at AP-C were within 2 m of the creek, while at AP-N the plots varied between 1-7 m from the creek.

Soil Organic Matter

Percent soil organic matter (% SOM) at Goose creek –created (GC-C), which was the oldest created marsh, was fairly constant with depth (Figure 4), as was % SOM at all of the natural sites. In the two younger marshes (AP-C and OS-C), % SOM decreased with depth.

Similarity between % SOM in the adjacent created and natural marshes increased with the ages of the created marshes. Percent SOM was significantly positively correlated with marsh age at all depths (Table 2). Increased age explained 40% of the variation in SOM in the top 2 cm, and 74% of the variation in SOM at 10-20 cm depth. A regression of marsh age and % SOM at each depth was used to produce equations to predict the age at which % SOM at a given depth should match the mature marshes (Fig. 5). The required age increased with depth from 20-25 years in the top 2 cm of soil, to 45-50 years in the 10-20 cm range. Percent SOM was also positively correlated with distance from the creek edge at all depths (Table 2).

Porewater Nutrients

NH_4^+ concentration differed significantly between sites, but not by marsh type in the fall or the winter (Table 3). NH_4^+ concentrations were generally highest in the spring (Fig 6A), although this pattern did not hold at OP-N, which tended to have the highest $[\text{NH}_4^+]$. AP-C and AP-N tended to have the lowest $[\text{NH}_4^+]$. NH_4^+ concentrations were not significantly correlated with any of the CO_2 flux measurements (Table 2).

HS^- concentration differed significantly between sites, but not by marsh type in the spring (Table 3). $[\text{HS}^-]$ generally were lowest in the winter and higher in the spring and fall (Fig 6B). Fall $[\text{HS}^-]$ showed a significant negative correlation with both annual P and R (Table 2), suggesting that higher sulfide levels may be affecting P and R rates. $[\text{HS}^-]$ measured were very low, this suggests that there may have been a problem with the collection method. Samples were collected between 10-15 cm depth in the soil; this may not have been deep enough to find representative samples. Another possibility is that the porewater was exposed to oxygen during the collection process, and most of the HS^- was oxidized before it could be preserved.

Porewater salinity differed significantly by site, but not by marsh type (Fig. 6C, Table 3), and did not vary with distance to the creek. It was negatively correlated to yearly total production and yearly total NEE across all marshes (Table 2), suggesting that higher salinity may inhibit production in these marshes. Porewater salinity was more strongly correlated with yearly total production than with NEE.

Marsh Production and Respiration

Comparison of annual production: GC-N had the highest annual gross primary production (GPP) of all marshes (Fig. 7), as well as the highest annual net ecosystem exchange (NEE). The created marsh at this site (GC-C) had similar values for annual GPP, NEE, and respiration (R).

Annual GPP was somewhat higher in AP-C than in AP-N, however R and NEE were similar between the two marshes. OS-C had the highest annual R (Fig. 7) and the lowest annual NEE of all the marshes. OS-C had higher annual GPP than OS-N, but because it also had high respiration, the NEE in the created site was lower than in the natural site.

Annual P and R varied significantly with plot distance from the creek (Table 4). Both annual P and R also differed significantly by site, but not marsh type. Annual NEE did not differ significantly by either marsh site or type.

Comparison of monthly values: All marshes showed a decrease in NEE in the early spring (Fig. 8). Since I did not measure GPP in the early spring, NEE in these months was calculated strictly from R measurements. During this period, the decreased NEE is reflecting increasing respiration with rising temperature. All marshes were net heterotrophic in the winter and early spring, and became autotrophic in the late spring (May). NEE peaked in the mid-summer, but the exact timing of the peak varied among sites. The peak appeared to occur a month later at AP than at the other two sites, likely due to differences in sampling dates (Appendix 4). The OS June sample was only taken 1 day before the AP July sample, so even though the months are different, the NEE peak probably occurs at about the same time in all three marshes.

All marshes except for GC-N briefly became net heterotrophic in the late summer. At both GC-N and OS-N the NEE peaked strongly again in the fall, while neither adjacent created marsh showed this peak. At AP, both the created and natural marshes peak again in the fall, although the effect was stronger in the created marsh.

Comparison of created and natural marshes: A plot of the monthly NEE of created versus natural marshes (Figure 9) showed that all points fall close to a 1:1 ratio line indicating the created and natural marshes were functioning similarly in terms of NEE. The only exceptions occurred in August and September (at all sites), and October (at Air Power Park). When the distance of the mean value for each point from a theoretical 1:1 ratio line was calculated, all points were within one standard deviation except for the months of August and September (at all sites), and October (at Air Power Park).

GPP:R ratio: The GPP:R ratio did not differ significantly between marshes and there were no obvious relationships with marsh age or type.

DISCUSSION

Comparing NEE in created and natural marshes

Monthly NEE was very similar in the created and natural marshes regardless of age. This result is consistent with previous research that suggested above- and below-ground biomass in created and natural marshes is equivalent by the time the marsh is approximately 4 years old (Broome et al. 1986, Craft et al. 1999).

Seasonal patterns in the created and natural marshes were similar, except during the early fall. The variation between marsh types during August and September (and at AP, October) was about 2 standard deviations greater than the variation during all other months. At GC, the simplest explanation for these differences is related to plant community composition. The created marsh was dominated by *Scirpus robustus*, while the natural marsh was dominated by *S.*

alterniflora. *Scirpus robustus* plants senesced in the middle of August, while *S. alterniflora* remained green through the middle of September (personal observation), allowing the natural marsh to have higher NEE when soil respiration began to fall in September. Tall form *S. alterniflora*, which occurs at GC-N, typically has two periods of intense growth, one in the spring and one in the fall (Reidenbaugh, 1983; Dai and Wiegert, 1996).

At OS, there is no obvious explanation for these seasonal patterns; both marshes are dominated by *S. alterniflora*. A possible explanation at this site may be differences in porewater $[\text{NH}_4^+]$. OS-N had higher porewater $[\text{NH}_4^+]$ than OS-C during the time of the year when NEE was not similar in the two marshes. High nutrient concentration has been found to increase production in *S. alterniflora* plants (Dai and Wiegert 1997). This increased nutrient concentration may be related to differences in hydroperiod or porewater flushing between the two systems.

AP-N is the only natural marsh where a fall peak in NEE was not apparent, and was the only site with the short form of *S. alterniflora*.. The plants were very short (< 50 cm) except for the plot immediately next to the creek. Short form *S. alterniflora* growth typically peaks just once per year. AP-C has a plant community composed entirely of tall form *S. alterniflora*, and showed two peaks in NEE, although the fall peak was lower than the spring peak.

With the exception of GC-C, NEE dropped below zero in August. In most cases, this decrease in NEE was due to a spike in R and a simultaneous decrease in GPP during the month of August. These are similar to results found in a study of gas exchange in a tidal freshwater marsh of Virginia (Neubauer et al. 2000.), which reported R exceeding GPP in the late summer and throughout the fall. This depression in NEE is likely due to temperature, which peaked in August in 2001. R increased with temperature according to an average Q_{10} of 2.8 in this study.

High temperatures may also have increased evapotranspiration, raising porewater and surface salinity, which has a negative effect on photosynthesis (Bradley and Morris, 1990).

Comparing GPP:R ratio over the chronosequence

Our data showed no connection between marsh age and GPP:R ratio in tidal salt marshes. It did not support the hypothesis (Odum 1969) that the GPP:R ratio in mature marshes equals one. The GPP:R ratio in natural (mature) marshes covered a wide range of values, from >1 to almost 3. Interestingly, when plot-distance from the marsh was used to normalized values of GPP:R, the results were qualitatively consistent with Odum's (1969) hypothesis that GPP:R ratio is higher in young ecosystems, and decreases over time. Normalization was used to remove any variation between sites due to differences in hydroperiod and sediment flushing resulting from different tidal regimes. Plot-distance from creek is an imperfect estimator of hydroperiod and flushing, so the results from this normalization should not be given too much weight. However, these results do suggest that the application of this aspect of Odum's (1969) hypothesis to tidal salt marshes may merit further study.

Distance to creek vs. organic matter in soil

There was a positive relationship between the percent soil organic matter (% SOM) at all depths and the distance that the cores were from the creek channel (Table 2). Two processes may be responsible for this correlation: decreasing inorganic sediment deposition with increasing distance from the creek, and increased organic soil production with increasing distance from the creek. Inorganic sediment can be brought into a marsh by tidal overwash (Friedrichs and Perry, 2001). As the water moves over the marsh surface, stems slow the water's velocity (Yang,

1998), and the sediment settles out. As distance from the creek increases, the potential amount of sediment that can settle out of the water decreases, and the actual amount of deposition also decreases. Because more inorganic sediment is deposited near the creek, there is less dilution of soil organic matter by mineral sediments with increasing distance from the creek (Kastler and Wiberg, 1996; Ward et al., 1998).

Organic matter content with depth

In both the created and the natural marsh at Goose Creek, SOM content remained fairly constant over the depth of the core (Fig. 4A), which is expected for a mature marsh (Ward et al., 1998). In the created marsh at OS, %SOM decreased with depth, while in the natural marsh, %SOM was relatively constant with depth (Fig. 4B). The decrease in %SOM in the created marsh was fairly large and it represented the change from accumulated organic matter on the soil surface to the mineral parent material on which the marsh was created. This profile was typical of the % SOM profile in a young, developing marsh (Ward et al., 1998), as was the created marsh at Air Power Park. The SOM content at AP-N increased slightly with depth (see Fig. 4C), suggesting a change in local sediment loading or hydroperiod.

The created marshes showed an increase in organic matter with age, with the oldest created marsh, GC-C, having % SOM similar to the natural, mature marshes. The predicted age of soil maturity was 20 years in top layer and 40 yrs in lowest layer, which is somewhat higher than the 10-20 years that previous research would indicate (Piehler et al. 1998).

Salinity and Production

There was a negative relationship between porewater salinity and both primary production and net ecosystem exchange. The relationship was stronger for P than for NEE, probably because NEE also incorporates R, which according to our data, was not correlated with salinity. This is consistent with the idea that high salinity could decrease nitrogen uptake, which would affect photosynthesis (Bradley and Morris, 1990). High porewater salinity creates osmotic or specific ion stress that adversely affects root metabolism or can competitively exclude NH_4^+ ions. Because plants invest most of their leaf nitrogen in to photosynthesis, a decrease in the availability of nitrogen to the plants could greatly affect production.

Porewater salinity is probably affected by two factors in these marshes. Site salinity reflects the salinity of the river water that floods the site, and any contribution from groundwater discharge. Salinity is also affected by the amount of flooding, with a decrease in flooding resulting in an increase in evapotranspiration, particularly during the summer months. High evapotranspiration leads to high porewater salinity because the water is selectively removed from the porewater, increasing the salt to water ratio in the porewater.

CONCLUSIONS

We had three hypothesis regarding the development of created marshes: 1) NEE would decrease with marsh age, eventually leveling off at levels similar to those in mature sites; 2) Porewater nutrients (NH_4^+ and HS^-) would increase with marsh age until they had reached mature levels; and 3) SOM would increase with marsh age. We found that SOM was the only variable that was clearly related to increasing marsh age. Within the limits imposed by between-marsh variability, it seemed that aboveground biomass and gas exchange were established in <4

years, the age of our youngest marsh. This suggests that created marshes quickly replace the functions of natural marshes lost to development in terms of gas exchange and carbon sequestration (i.e. NEE).

In terms of net primary production, the created marshes were similar to their adjacent natural marshes on a month-to-month basis, except in the fall. This may be due to differences in plant community composition, differences in the porewater nutrient levels, or some factor outside of the scope of this study. This fall disconnect between the created and natural marshes would be an interesting area for further research.

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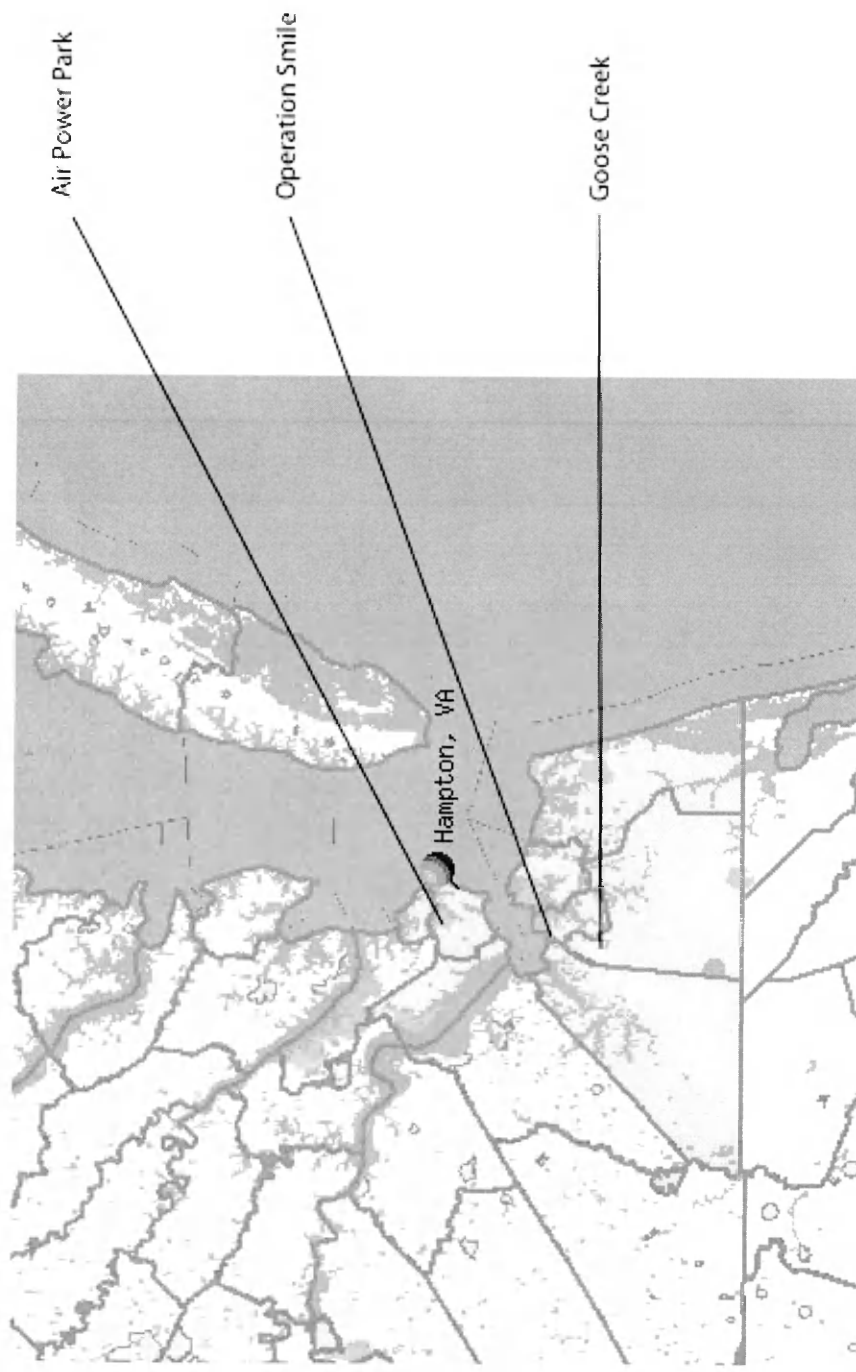


Figure 1. Map of marsh locations. Map of Virginia from Census Database at tiger.census.gov.

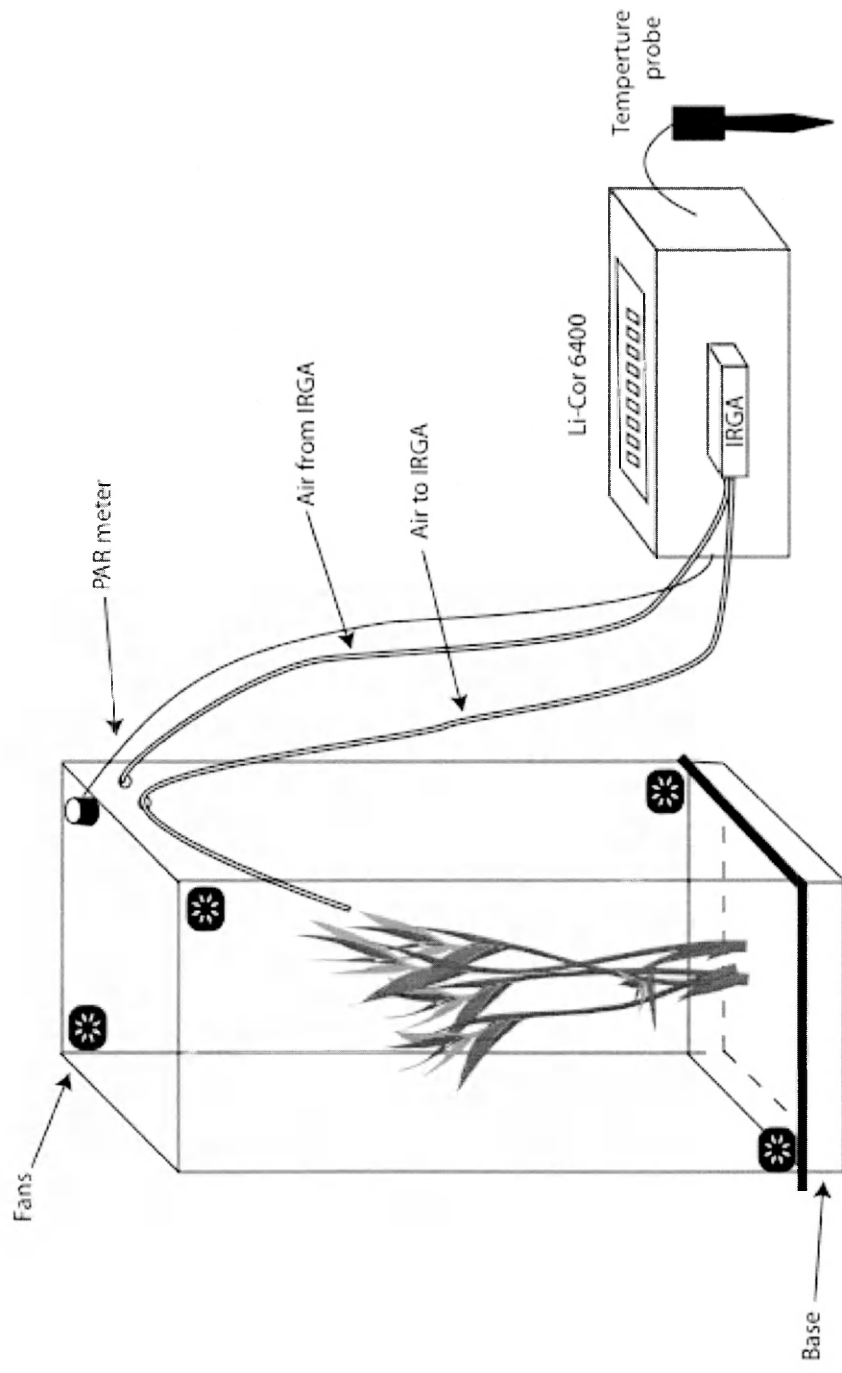


Figure 2. Diagram of carbon flux sampling equipment. Air is pulled from the chamber into the IRGA, where the CO_2 content is measured. The air is then returned to the chamber. A PAR meter and a temperature probe also gather information stored by the Li-Cor 6400.

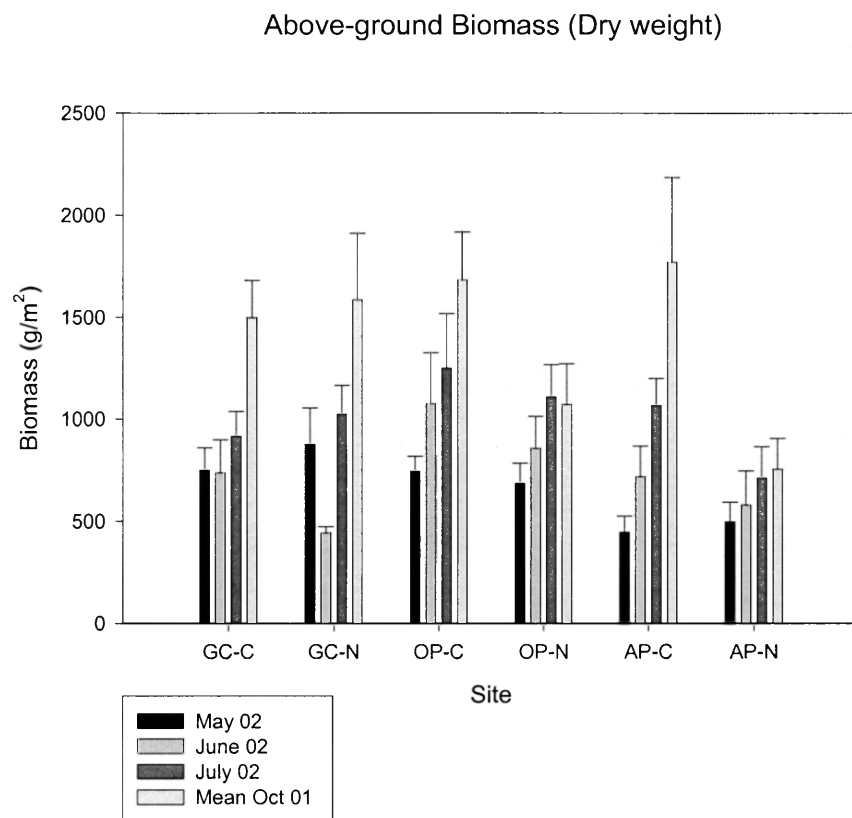


Figure 3. Above-ground biomass of marshes at different times of the year. October biomass was collected at the end of the 2001 growing season, other samples were collected during the 2002 growing season.

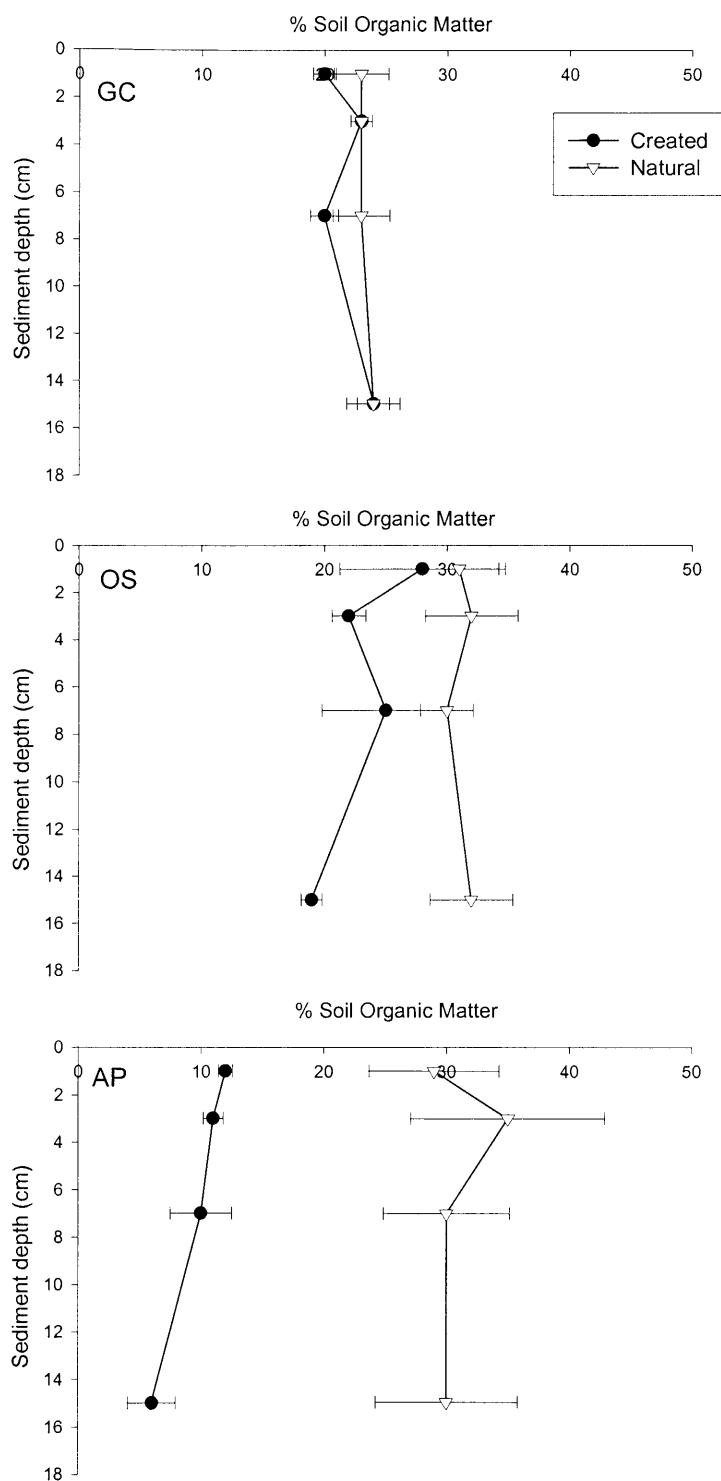


Figure 4. Soil Organic Matter Profiles. Organic matter content was measured at four depths, points represent the mean percent organic matter, and bars are one SEM.

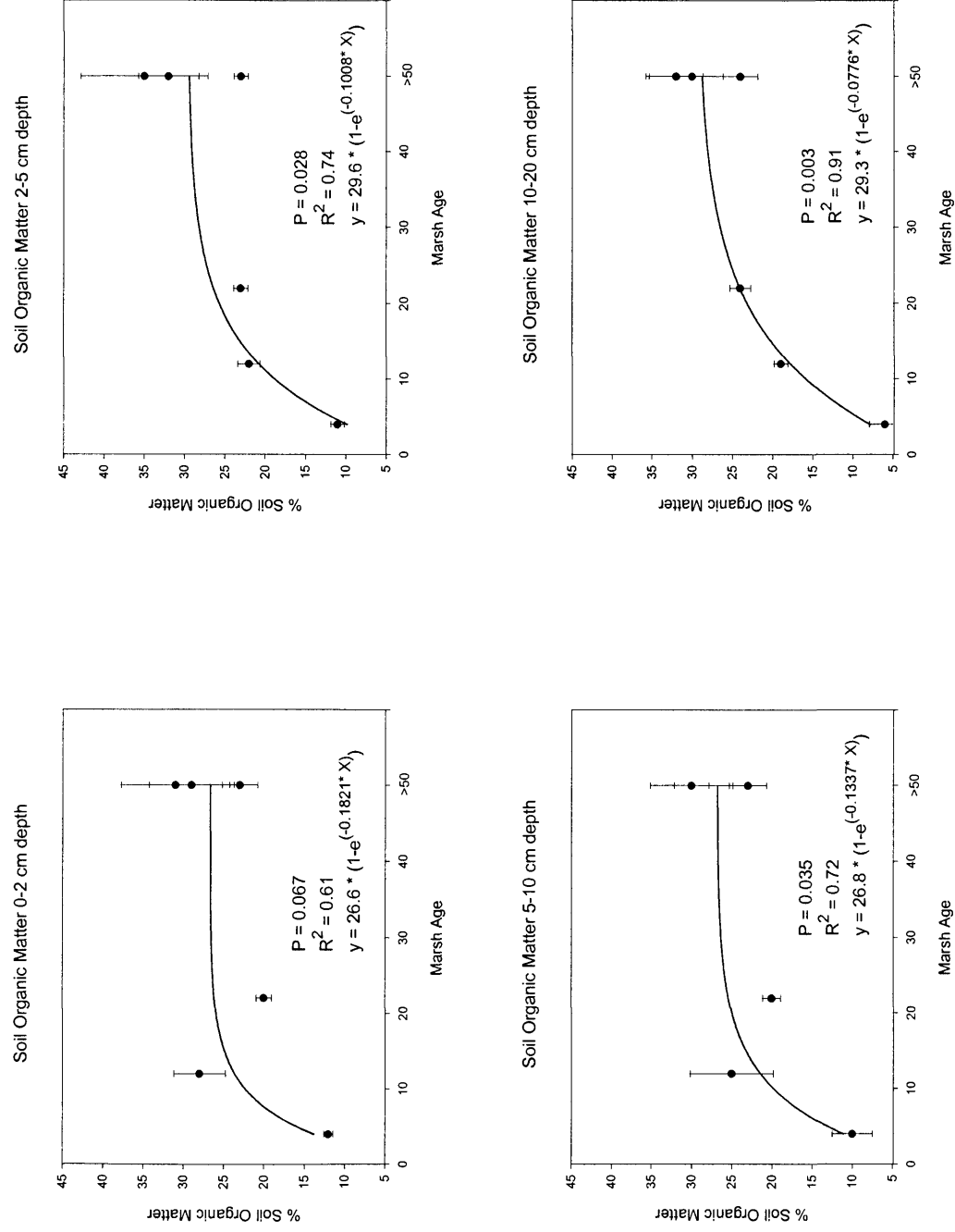


Figure 5. Soil organic matter vs. marsh age at four different sediment depths. Points represent means, and error bars represent SEM.

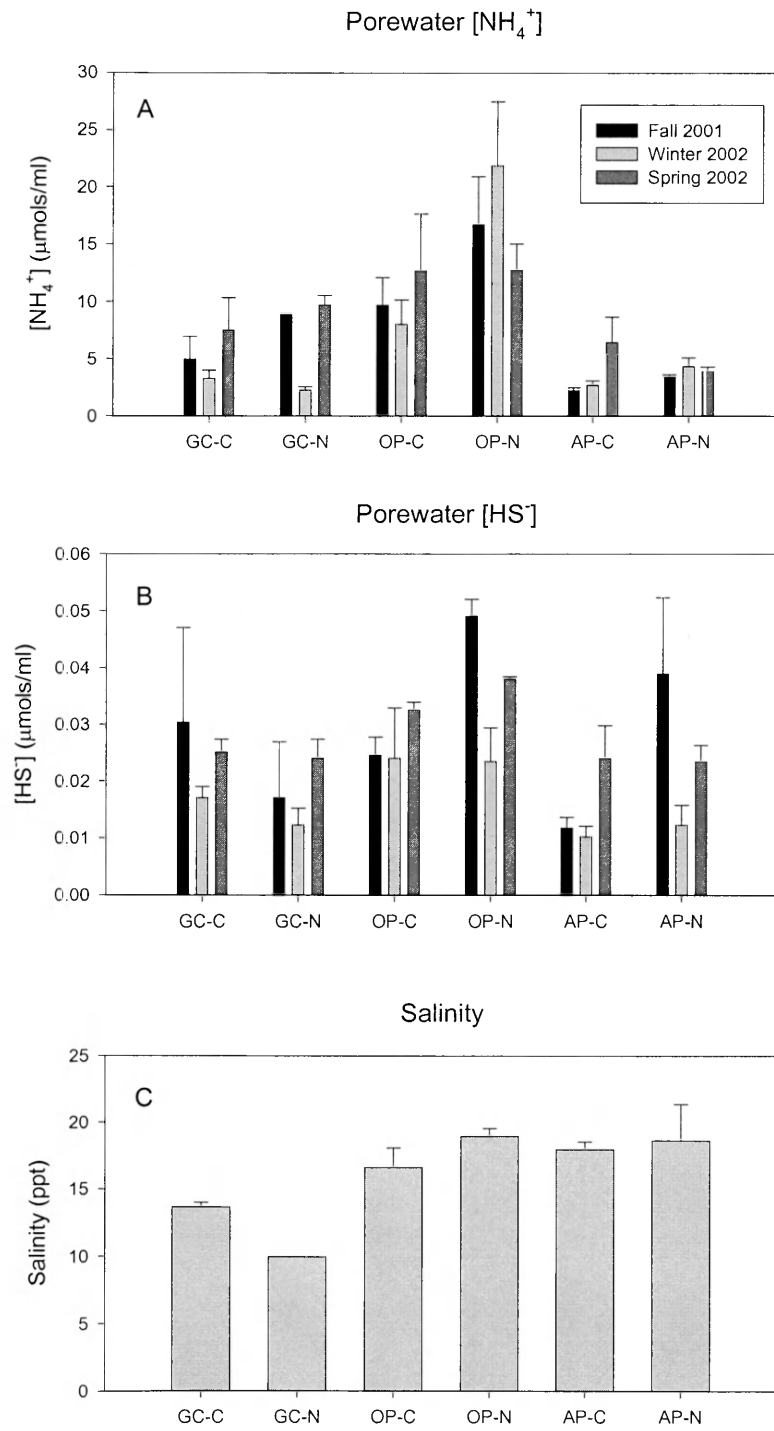


Figure 6. Porewater Nutrient Values. NH_4^+ and HS^- were measured on three occasions, and salinity was measured once. Bars represent the mean values, and error bars represent 1 SE.

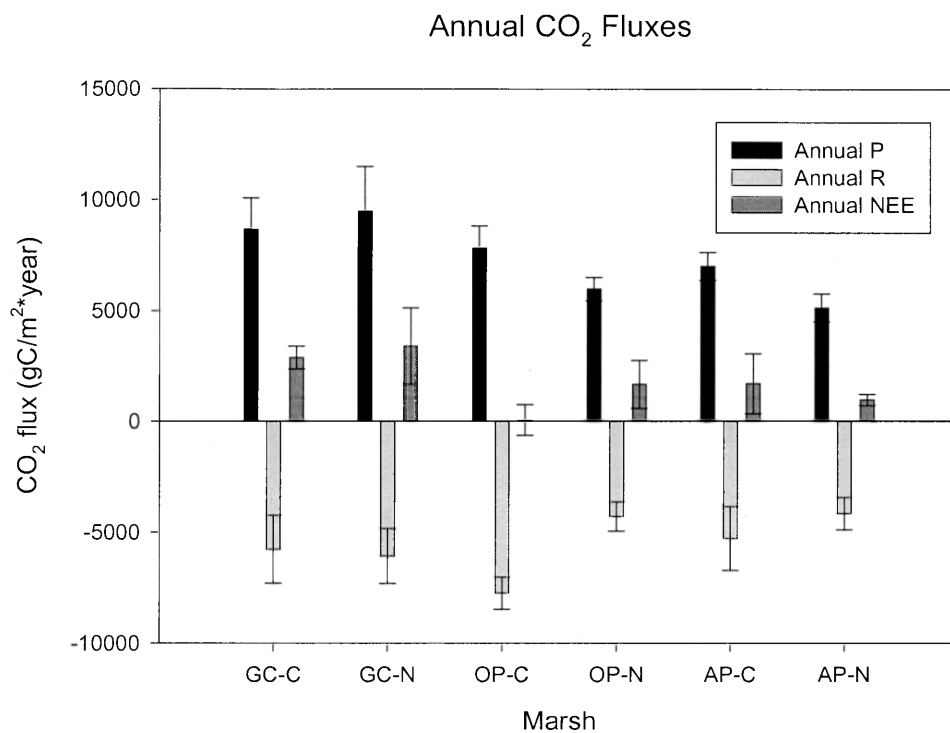


Figure 7. Annual photosynthesis, respiration, and net ecosystem exchange. Bars represent the mean CO₂ flux in each marsh, and error bars represent one SEM.

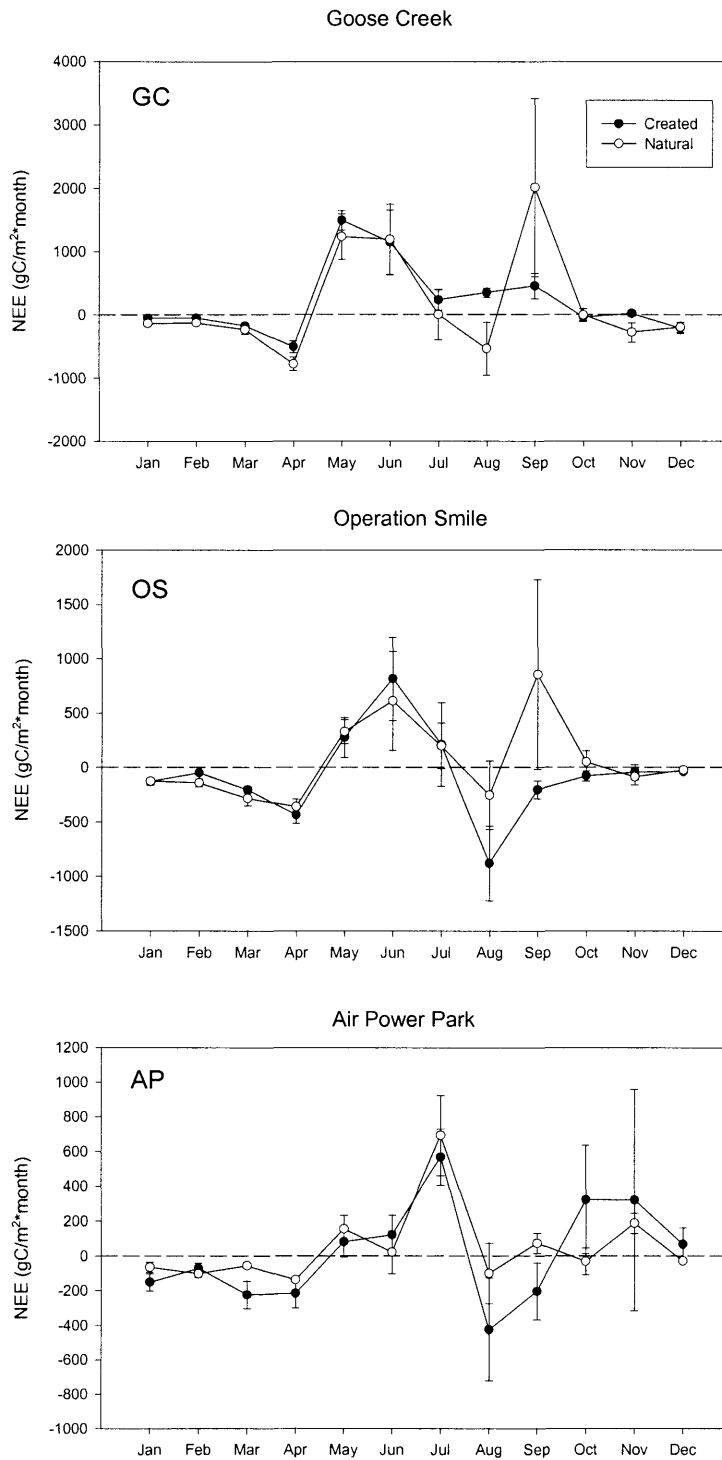


Figure 8. Monthly NEE at each marsh. Created and natural marshes at each site are placed on the same graph, the points represent mean monthly NEE, and the bars are 1 SE. The dotted line is a reference line showing GP=R.

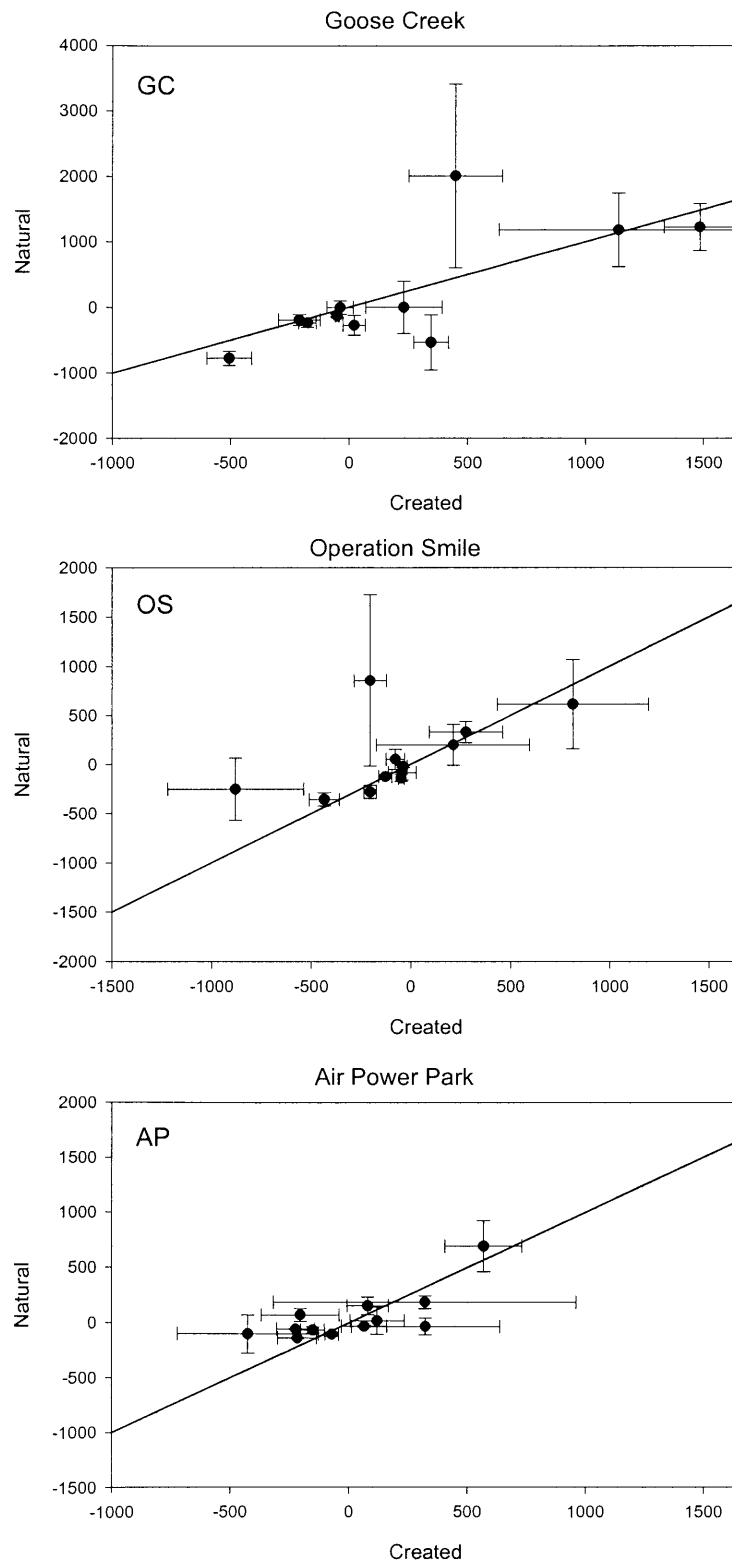


Figure 9. Ratio of NEE in Created and Natural Marshes. Line shows a theoretical 1:1 ratio line.

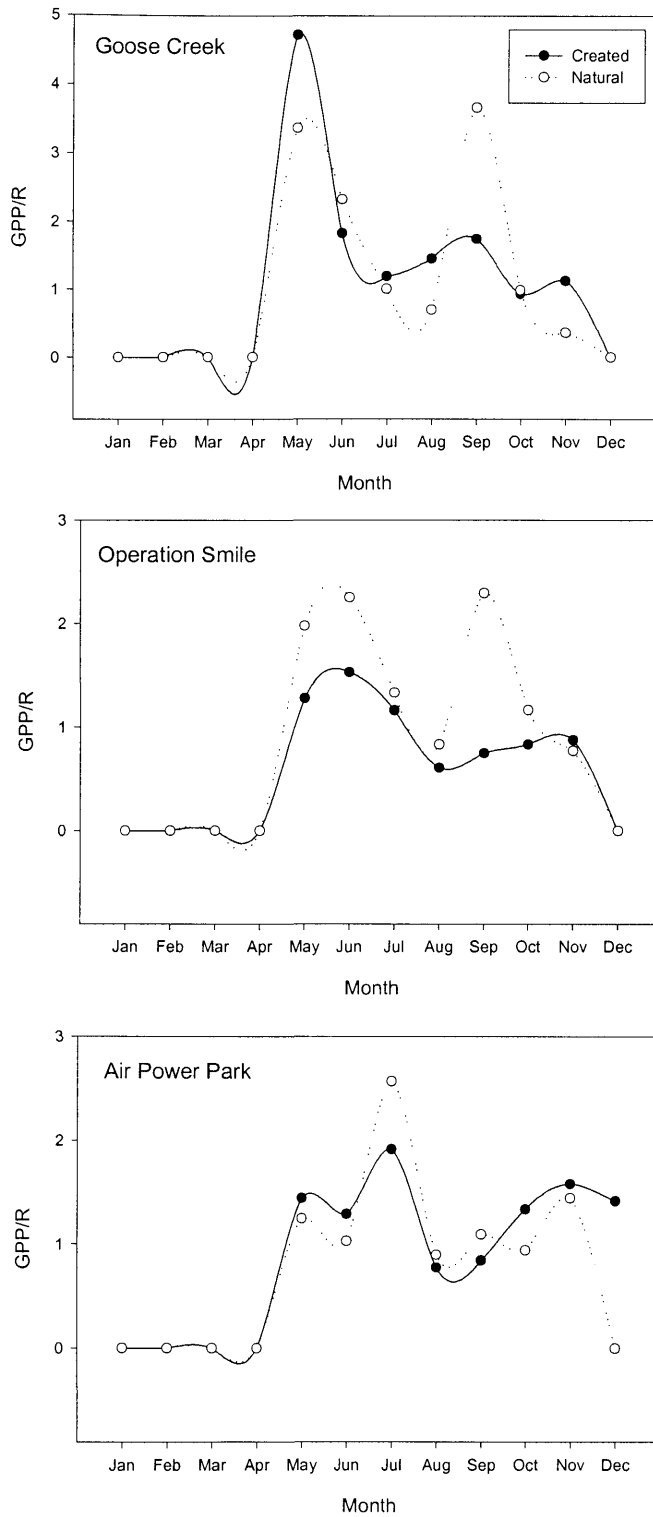


Figure 10. Ratio of GPP to R in each marsh. Closed circles represent created marshes, open circles represent natural marshes.

Table 1. ANOVA table. Fixed factors are Site (GC, OS, AP) and Type (C and N), the co-variate is plot distance from creek, N = 5.

Flux variable	Source	Df	MS	F statistic	P-value
Biomass (Oct 2001)	Distance	1	1553364.293	5.041	0.035*
	Site	2	770358.269	2.500	0.104
	Type	1	707479.635	2.296	0.143
	Site*Type	2	684090.242	2.200	0.131
	Error	23	308115.907		
SOM (0-2 cm)	Distance	1	170.027	2.408	0.134
	Site	2	151.251	20142	0.140
	Type	1	179.938	2.548	0.124
	Site*Type	2	176.290	2.497	0.104
	Error	23	70.606		
(2-5 cm)	Distance	1	176.435	2.541	0.125
	Site	2	86.040	1.239	0.308
	Type	1	681.553	9.816	0.005*
	Site*Type	2	302.657	4.359	0.025*
	Error	23	69.434		
(5-10 cm)	Distance	1	130.857	1.797	0.193
	Site	2	99.769	1.370	0.274
	Type	1	405.307	5.567	0.027*
	Site*Type	2	209.287	2.874	0.077
	Error	23	72.810		
(10-20 cm)	Distance	1	94.957	2.156	0.156
	Site	2	65.449	1.486	0.247
	Type	1	1077.753	24.468	<0.001*
	Site*Type	2	191.005	4.336	0.025*
	Error	23	44.048		

* = significant at 0.05

Table 2. Pearsons correlation coefficients for soil and gas exchange variables.

Parameter [†]	Age	Distance to creek	P	R	NEE
NH ₄ ⁺					
Fall	0.364	0.297	-0.072	-0.208	0.122
Winter	0.186	0.123	-0.371	-0.297	-0.138
Spring	0.184	-0.124	0.115	0.267	-0.130
HS ⁻					
Fall	0.404	0.599*	-0.693**	-0.495*	-0.319
Winter	-0.004	0.208	-0.124	-0.168	0.022
Spring	0.090	0.293	-0.136	-0.310	0.148
Salinity	-0.120	-0.129	-0.512*	-0.056	-0.543*
SOM					
0-2 cm	0.405*	0.407*	-0.204	-0.106	-0.122
2-5 cm	0.597**	0.363*	-0.351	-0.340	-0.045
5-10 cm	0.511**	0.389*	-0.191	-0.108	-0.106
10-20 cm	0.738**	0.468**	-0.304	-0.288	-0.046
P	-0.261	-0.126	-----	0.589**	0.528**
R	-0.120	-0.416*	0.589**	-----	0.374*
NEE	0.137	0.292	0.528**	-0.374*	-----

[†] correlation based on n = 3 for NH₄⁺, HS⁻ and salinity, otherwise n = 5

* = significant at the 0.05 level, ** = significant at the 0.01 level

Table 3. ANOVA tables for porewater nutrient variables. Fixed factors are Site and Type, the co-variate is plot distance from the creek, N = 3.

Flux variable	Source	Df	MS	F statistic	P-value
[NH₄⁺]					
Fall	Distance	1	0.261	0.542	0.477
	Site	2	2.418	5.021	0.028*
	Type	1	1.430	2.969	0.113
	Site*Type	2	0.0492	0.102	0.904
Winter	Distance	1	0.0636	0.125	0.730
	Site	2	3.527	6.929	0.011*
	Type	1	0.566	1.112	0.314
	Site*Type	2	0.537	1.055	0.381
Spring	Distance	1	2.812	3.993	0.071
	Site	2	1.966	2.791	0.105
	Type	1	1.668	2.369	0.152
	Site*Type	2	0.383	0.544	0.595
[HS⁻]					
Fall	Distance	1	0.00157	9.162	0.012*
	Site	2	0.00039	2.315	0.145
	Type	1	0.00010	0.594	0.457
	Site*Type	2	0.00074	4.333	0.041*
Winter	Distance	1	0.000001	0.016	0.903
	Site	2	0.00021	2.706	0.111
	Type	1	0.000006	0.081	0.781
	Site*Type	2	0.000018	0.236	0.794
Spring	Distance	1	0.000006	0.189	0.672
	Site	2	0.000217	6.748	0.012*
	Type	1	0.000002	0.071	0.795
	Site*Type	2	0.000018	0.545	0.595
Salinity					
Salinity	Distance	1	7.127	1.429	0.257
	Site	2	79.634	15.964	0.001*
	Type	1	2.094	0.420	0.530
	Site*Type	2	13.711	2.748	0.108
	Error	11	4.988		

* = significant at 0.05

Table 4. ANOVA table for total annual values of CO₂ flux variables (P, R, and NEE). Fixed factors are Site (GC, OS, AP) and Type (Created and Natural), the co-variate is plot distance from the creek, N = 5.

Flux variable	Source	Df	MS	F statistic	P-value
Annual P	Distance	1	26909156.950	4.582	0.043*
	Site	2	37267635.901	6.346	0.006*
	Type	1	244392.439	0.042	0.840
	Site*Type	2	3965044.394	0.675	0.519
	Error	23	5872169.834		
Annual R	Distance	1	65510343.234	18.184	<0.001*
	Site	2	28918733.094	8.027	0.002*
	Type	1	357113.448	0.099	0.756
	Site*Type	2	3559073.821	0.988	0.388
	Error	23	3602663.161		
Annual NEE	Distance	1	8447407.030	1.518	0.230
	Site	2	12828712.080	2.305	0.122
	Type	1	10656.239	0.002	0.965
	Site*Type	2	2608607.063	0.469	0.632
	Error	23	5566031.553		
GPP:R	Site	2	9.705507	3.083803	0.064
	Type	1	5.862299	1.862672	0.185
	Site*Type	2	5.628472	1.788376	0.189
	Error	24	3.147253		

* = significant at 0.05

Appendix 1: Specific Hypothesis

(H₀1) Net ecosystem exchange (NEE): NEE is directly related to temperature.

NEE is expected to be highest in the young created marsh, and lowest in the older, natural marshes.

Temperature affects both respiration and photosynthesis (Knorr 2000), so it is expected they will be higher in the summer than in the winter. Photosynthesis should be highest when leaf area is greatest; therefore, photosynthesis should be highest in the late summer. Respiration rates are highly coupled to temperature, so they should be highest in the summer when the air and soil temperatures are high.

In a young, developing ecosystem, production is usually higher than respiration, while in a mature system production and photosynthesis are approximately equal (Odum 1969). Therefore, in a young marsh, the net ecosystem exchange (photosynthesis + respiration) should be high since photosynthesis (CO₂ flux in to the plant) will be higher than respiration (CO₂ flux out of the plant). In a mature marsh one would expect that net ecosystem exchange should be lower, since photosynthesis and respiration should balance each other. Hydrogen sulfide content of the soil may also affect the rate of photosynthesis in the marsh by affecting plant nutrient uptake. Since the created marshes are expected to have lower levels of hydrogen sulfide in the soil (see below), it supports the idea that the created marshes should have higher rates of photosynthesis and thus higher net ecosystem exchange.

(H₀2) Porewater nutrients: NH_4^+ and HS^- concentration should increase with marsh age and therefore should be highest in the natural marshes.

Mean NH_4^+ concentration in porewater has been shown to increase over time in salt marshes (Tyler and Zieman 1999). Therefore, the natural marshes would be expected to have higher NH_4^+ concentrations than the created marshes although this may not be true for the oldest created marsh, Goose Creek. A pattern of increasing NH_4^+ concentration with marsh age may also be seen in the created marshes.

Higher concentrations of HS^- are expected in the natural marshes than in the created marshes. Natural marsh soils have been anoxic for a longer period of time, and would have been inundated longer than the created marsh soils. The created soils may have larger grain size than the natural ones, leading to more aerated soils. Natural marshes also may have more organic material buried in the soil and available for microbial decomposition. Created marshes are usually graded from uplands soils, and therefore they may have higher concentrations of Fe. Iron can bind to the sulfur in HS^- to form pyrite (FeS_2); pyrite can effectively remove sulfide from the soils.

(H₀3) Soil organic matter: Natural marshes are expected to have the highest soil organic matter. The youngest created marsh is hypothesized to have the lowest soil organic matter content, and OM should increase with marsh age in the created marshes.

As NH_4^+ concentration increases in the porewater, the %N in *S. alterniflora* tissue increases (Anderson et al. 1997). When plants die they are incorporated into the soil, increasing the amount of organic N in the soil. Therefore, higher organic N content is expected in the soil of the natural marshes. The incorporation of plants into the soil with each growing season can change other soil characteristics, as well, including higher organic C content in the natural marshes and lower bulk density, and a lower C:N ratio. In the created marshes, bulk density is expected to increase with depth as the soils surface organic matter content is expected to increase over time. In the natural marshes, bulk density should remain constant with depth since the marshes have been producing similar levels of organic matter over the years.

Literature Cited

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Appendix 2: Measuring CO₂ flux

Two methods have been used to estimate primary production in salt marshes: 1) CO₂ flux and 2) standing biomass. CO₂ flux has three advantages over the standing biomass method. First, it measures production and respiration within a portion of the ecosystem, not just the plant component of the ecosystem. Second, it directly measures the flux of carbon in and out of the ecosystem. Therefore, it simultaneously measures aboveground and belowground productivity (Steever et al., 1998), and also measures productivity and respiration of microbial mats and soil organisms. Third, the accuracy of CO₂ flux methods are not affected by high rates of turnover or by mixed species composition.

Working with a chamber system similar to ours, Steever et al. (1998) found that CO₂ flux methods are potentially more accurate than biomass methods. When they compared NEE and respiration measurements (from CO₂ flux) they found both to be strongly related to biomass measurements. They also found that when biomass was absent from a plot, NEE was very close to zero, (they attributed the slight NEE measurement to random error). This relationship supports the hypothesis that CO₂ flux methods accurately measure production. In a conservative analysis of accuracy, they found the CO₂ flux to give errors of about 90 gC/m²yr (or about 10% of yearly production). They analyzed the precision of the chamber method by looking at repeated measures of CO₂ flux over a range of productivities found in the field, and found the method to be precise.

Problems associated with closed chamber CO₂ flux methods include: 1) CO₂ flux rates can be affected by temperature and humidity, and in a closed chamber both of these

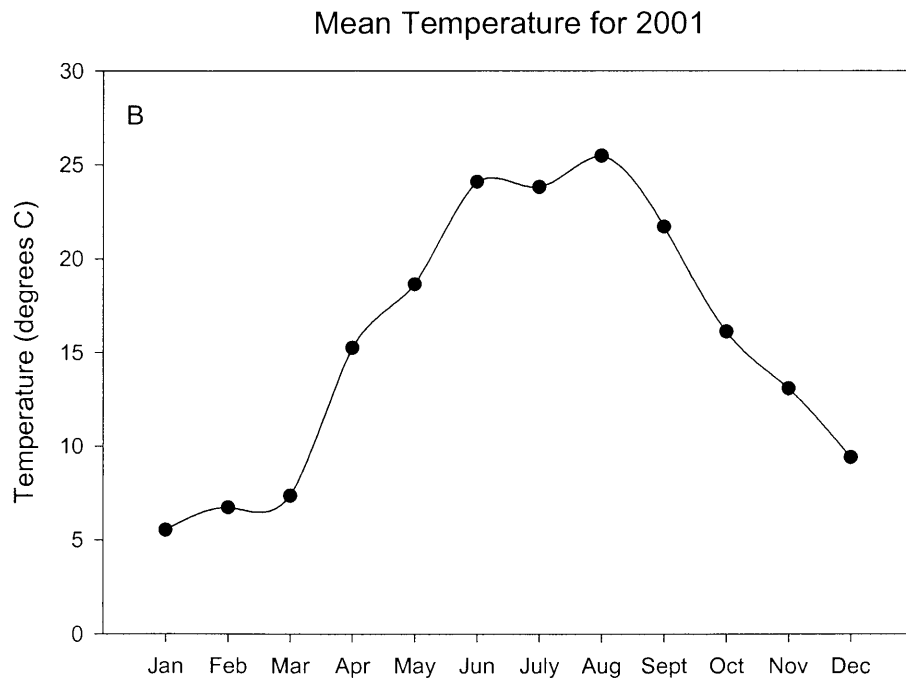
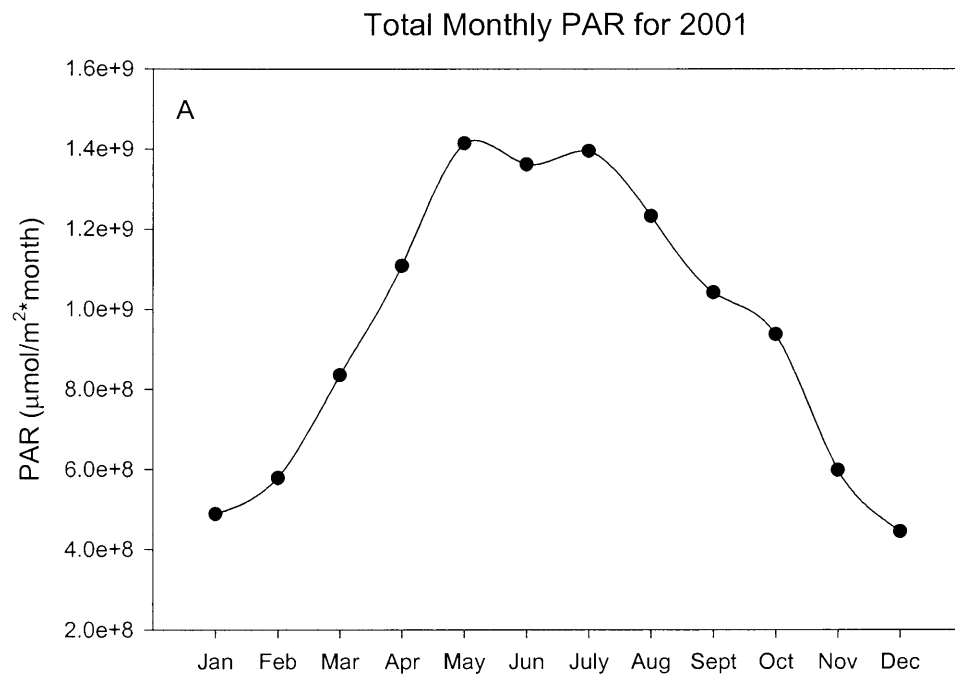
tend to increase. We attempted to mitigate this problem by keeping measurement times as short as possible (for an accurate measurement) and by airing the chamber out between readings. 2) The rate of CO₂ flux is also affected by CO₂ concentration in the chamber. As plants photosynthesize, they drawdown the ambient CO₂ concentration in the chamber, and as ambient CO₂ concentration decreases, the rate of photosynthesis decreases. Again we used short measurement times (15-60 sec) to mitigate for this problem, and aired the chamber out between sets of measurements to return the CO₂ concentration inside the chamber to the ambient concentration outside the chamber (generally around 350 ppm). 3) Since the chambers were portable, they may not seal off the interior completely, and mixing of gases may occur. Steever et al. (1998) found that the foam rubber gasket at the base of the chamber prevented much mixing with the atmosphere. We had similar results in indoor tests. 4) Because we were modeling CO₂ flux against PAR, clouds were a problem. Clouds could temporarily lower the PAR reading, without immediately lowering CO₂ flux. This could result in a slight overestimation of NEE since the PAR reading would be lower than the actual PAR-CO₂ flux relationship. 5) The chamber may artificially increase shading in the plots by compacting the plant leaves together. The PAR readings were taken from the top of the chamber; in the early spring this may have lead to an underestimation of NEE because the young plants may have been shaded by dead plant material from the previous year. Therefore, the young plants may have actually received less light than the PAR readings indicated. 6) Measuring the CO₂ flux at each site took several hours. During this time the temperature may rise and could affect the CO₂ flux in the later plots compared to the earlier plots. We used the measured temperature and CO₂ flux for each plot when

modeling the respiration to control for this problem. 7) Any water covering the sediment surface would interfere with the CO₂ flux from the sediment. Therefore, CO₂ flux was measured at low tide. 8) If the ambient light level is too low, the resulting equation (PAR vs. CO₂ flux) will be a straight line rather than a hyperbola; therefore we collected data on sunny days whenever possible, and in the middle of the day when the sun was at its highest point. Despite this, the equation describing the relationship between PAR and CO₂ flux was a straight line for some plots in some months.

Literature Cited

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Appendix 3. Graphs of ambient conditions as measured at the Virginia LTER site on the Eastern Shore of Virginia. Graph (a) shows the total monthly PAR for the year 2001, graph (b) shows mean monthly temperatures for the year 2001.

Appendix 4. Sampling dates for CO₂ flux measurements.

Marsh	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sept	Oct	Nov	Dec
GC	17	23	23	22	17	17	14	15	14	11	13	12
OS	16	24	27	19	30	30	31	28	28	26	30	28
AP	20	8	22	20	1	3	1	16	12	12	31	1